2015

Assessing the ecohydrological impact of incorporating perennial vegetation into an agricultural watershed in Central Iowa, USA

Vilma Salome Mateos Remigio
Iowa State University

Assessing the ecohydrological impact of incorporating perennial vegetation into an agricultural watershed in Central Iowa, USA

by

Vilma Salome Mateos Remigio

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Environmental Science

Program of Study Committee:
Richard C. Schultz, Co-Major Professor
Heidi Asbjornsen, Co-Major Professor
Thomas J. Sauer
Matthew J. Helmers
Jesse A. Randall
Julie M. Tarara

Iowa State University

Ames, Iowa

2015

DEDICATION

To my grandparents Inocencia Hermenegildo and Jacinto Mateos: thanks for your love, protection, support, and for giving me the freedom to choose my own path. To my family and friends: thanks for believing in me.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 5

LIST OF FIGURES

Page

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

ACKNOWLEDGEMENTS

I want to thank to Dr. Heidi Asbjornsen and Dr. Matt Helmers for letting me be part of the STRIPs project and giving me the opportunity to pursue a graduate degree. I want to express my most sincere appreciation to Dr. Richard Schultz and Dr. Tom Sauer for guiding me throughout my dissertation work and I thank them for all the support and time they provided me. I would like to further extend my gratitude to Dr. Jesse Randall and Dr. Julie Tarara for their support and advice.

Special thanks to Chris Witte, Forrest Goodman and David Williams for their help and technical support. Many thanks to the students who were involved in the project and that helped me in the field, greenhouse, and lab activities. Those students were: Gabriela Lopez, Indira Ortiz, Adan Hernandez, Nate Looker, Omar de Kok-Mercado; Brian Noonan, and Tomorra Smith.

Finally I want to thank to Dr. Salvador Lozano Trejo for believing in me and encouraging me to pursue my Ph.D. degree.

ABSTRACT

Iowa's tallgrass prairies, the once dominant vegetation, were replaced by crops so that currently, only 0.1% of native prairies remain and approximately 80% of the land is dedicated to corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.) production. This dramatic land use change has caused severe hydrological alterations (i.e. surface runoff, sediment and nutrient export) affecting the productivity and water quality of the region. In the last years, incorporation of prairie vegetation within agriculturally dominated watersheds has been demonstrated to have positive effects on restoring hydrologic balance by increasing soil water infiltration and nutrient stabilization. However, less attention has been given to the impact that plant water use from native perennial vegetation might also have on stabilizing hydrologic processes. This study aimed to increase our knowledge about water use patterns in native prairies and crops, at both the stand (evapotranspiration) and plant (transpiration) level, in order to enhance our understanding of the potential role of introduced prairie ecosystems on hydrologic regulation. To accomplish the objective, two field studies were conducted at the Neal Smith National Wildlife Refuge located in Central Iowa, and one study was conducted in the Forestry greenhouse at Iowa State University. Micrometeorological, thermometric and physiological techniques were used to measure plant water use rates and understand water use patterns. Overall, prairie vegetation exhibited higher evapotranspiration than crop fields early and late in the season, suggesting a higher efficacy by the former to increase the soil water storage capacity during typical wet springs, which would help to reduce runoff. At the plant level, transpiration of native prairie species higher responsiveness than crops to changes in soil water content and a significant increment in water uptake was

observed following water inputs preceded by dry periods at both field and greenhouse conditions. We conclude that prairie vegetation can help to restore hydrologic processes in agricultural landscapes by extracting more water from the soil when soil water holding capacity is most needed.

CHAPTER 1: GENERAL INTRODUCTION

The Midwestern United States, also called Corn Belt, including all or parts of Illinois, Indiana, Iowa, Michigan, Minnesota, Ohio and Wisconsin, is one of the most productive regions in the world and has a critical role in the US economy (Hatfield, 2012). The 2012 Census of Agriculture reported that the Midwestern States had a market value of agricultural products of $110,986,197,000 (USDA Census of Agriculture, 2012). Among those states, Iowa ranked first with $30,821,532,000. Such high productivity has been achieved in part at the expense of replacing most of the native tallgrass prairie that once dominated the landscape. In Iowa, only about 0.1% of the native prairie remains (Samson and Knopf, 1994) and approximately 80% of the state land is dedicated to corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.) production (Burkart et al., 1994). Nonetheless, the region is currently facing several hydrological issues as a consequence of the large scale land conversion, and the effects of climate change.

Tallgrass prairies are a highly diverse ecosystem, with two functional groups representing plants species composition: C_3 forbs and C_4 grasses (Fay et al., 2002). These groups exhibit different traits in phenology, aboveground morphology, and physiology (Ode et al., 1980; Turner et al., 1995; Fay et al., 2002). Growing season activity in prairie ecosystems is started by C_3 forbs early in the spring (Ode et al., 1980) when low temperatures and high water availability satisfy the requirements of this functional group (Black, 1971;Turner et al., 1995). As temperature increases and soil water content becomes limited, dominance of C_3 species is replaced by C_4 grasses (Ode et al., 1980) that have lower water and higher temperature requirements, and also need high irradiance for light saturation

(Black, 1971; Kemp and Williams, 1980). Primary production is maintained by the C_4 grasses until the end of summer when C_3 forbs again become the dominant producers. Belowground, tallgrass prairies also have unique attributes. Approximately 2/3 of the total plant biomass occurs belowground (Rice et al., 1998), and species have deep roots, with forbs exhibiting deeper roots than grasses (Weaver, 1954). These characteristics are responsible for producing soils of high physical quality, expressed as good soil structure, low bulk density (Jastrow, 1987; Baer et al., 2002), and high infiltration rates (Guzman and Al-Kaisi, 2011).

After native prairie vegetation was replaced by annual crops that have a shorter growing season and less root biomass, soils were left vulnerable to erosion. The structure of the soils was also modified as mechanized agriculture increased bulk density and decreased soil water infiltration rates (Brye and Pirani, 2005;Udawatta et al., 2008; Guzman and Al-Kaisi, 2011). Thus, surface runoff and sediment and nutrient export developed into a serious environmental issue that has affected productivity and surface water quality. The effect of agriculture in the Midwest has been aggravated by an increase in the frequency and magnitude of extreme precipitation events (Todd et al., 2006; Groisman et al., 2012; Villarini et al., 2013).

The Conservation Reserve Program (CRP) was authorized by the 1985 Farm Bill as a strategy "to re-establish valuable land cover to help improve water quality, prevent soil erosion, and reduce loss of wildlife habitat" (www.fsa.usda.gov). Through this program, farmers are reimbursed for removing land from agricultural production and establishing conservation practices such as riparian buffers, filter strips and contour grass strips, among others that are established with perennial vegetation. In Iowa, reintroduction of perennial

strips at strategic locations within agricultural watersheds has been shown to have a significant impact on reducing surface runoff (Hernandez-Santana et al., 2013) and sediment (Helmers et al., 2012) and nutrient export (Zhou et al., 2014), as well as decreasing nitrate-nitrogen concentration in the vadose zone and shallow groundwater (Zhou et al., 2010). Generally, the higher infiltration rates of soils supporting perennial vegetation are assumed to be responsible for enhancing those hydrologic processes. The plant density in the perennial strips, that is higher than in the crop fields, has also been found to help slow surface runoff velocity (Meyer et al., 1995) and trap sediment (Ghadiri et al., 2001). Moreover, native prairie species are more efficient at stabilizing nutrients in the biomass and soil, which may contribute to the reduction of their export (Perez-Suarez et al., 2014). Although vegetation water use is the largest component of the hydrologic cycle (Schlesinger and Jasechko, 2014), the direct impact that plant transpiration may have on mitigating the negative consequences of agricultural activities is often ignored.

The dramatic conversion of native prairies to annual crops altered seasonal patterns of soil water evaporation and plant transpiration because prairies have a longer growing season than most annual crops and start transpiring earlier in spring and finishing later in the fall (Brye et al., 2000). Particularly the earlier activity by prairie species compared to crops may contribute to reducing surface runoff, as the earlier water consumption decreases soil water content and increases soil water storage capacity during the wettest months of the year. Another advantageous attribute of native prairie species over annual crops is related to their deeper roots that enable them to access water from deeper soil layers, and hence, maintain lower water tables (Schilling and Jacobson, 2010). Thus, the water use patterns modified by replacing perennial vegetation with annual crops have been suggested to have contributed to

increased baseflow (Zhang and Schilling, 2006; Schilling et al., 2008) and surface runoff (Schilling et al., 2008; Hernandez-Santana et al., 2013). Furthermore, studies conducted at the leaf level have shown that water use of native prairie species can increase dramatically in response to increaseing soil water content that occurs after a dry period (Martin et al., 1991; Swemmer et al., 2006). In contrast, corn and soybean usually exhibit a delayed response (Guo et al., 1998; Hura et al., 2006; Wang et al., 2006). A higher responsiveness by prairie species suggest that they might also be more helpful to reduce runoff than the crops, as the drawdown of soil water increases soil water storage capacity again prior to the next precipitation event.

Despite the potential positive effects that plant water use may have on stabilizing hydrological processes, it is particularly notable that there is a lack of comparative studies that address water use patterns in native prairie ecosystems and annual crop fields. Given the increased interest of incorporating perennial species into agricultural watersheds, it is imperative that we understand to the differences in plant water use dynamics, either as evapotranspiration or transpiration, in both prairie and annual crop vegetation.

The objectives of this dissertation research were: 1) to assess simultaneous plant water use at the stand (evapotranspiration) and plant (transpiration) level in prairie vegetation and annual crop fields; and 2) to assess the response of native prairie species and annual crops to increased soil water content that was preceded by moderate and severe water stress conditions. The goal was to enhance our understanding of the role of introduced prairie ecosystems on hydrologic regulation. To accomplish the first objective, two studies were conducted under field conditions at the Neal Smith National Wildlife Refuge (NSNWR) located in Jasper, County Iowa, in 2007-2008 and 2011-2012. For the second objective, a

study was performed under controlled conditions in the Forestry greenhouse at Iowa State University in 2013.

Dissertation Organization

This dissertation is organized into 6 chapters. Chapter one is the general introduction. Chapter two is a paper that describes seasonal evapotranspiration patterns in a restored prairie and an agricultural field measured throughout the growing seasons of 2007 and 2008; as well as results of plant transpiration measured during the peak growing season in 2008. Chapters 3 and 4 correspond to the second field study conducted in a mixed annual-perennial watershed over different periods in the growing seasons of 2011 and 2012. In chapter three the main environmental drivers of hourly transpiration are identified. Chapter four is a paper that describes plant transpiration dynamics in strips of prairie vegetation and adjacent crops placed at two topographic positions; and it also discusses the possible implications on watershed hydrology. Chapter five describes the results of a greenhouse experiment that explored the response of two native prairie species and two crops to rewatering after being subjected to two different water stress levels. Chapter 6 is the general conclusion of this research.

References

Baer, S.G., Kitchen, D.J., Blair, J.M.,Rice, C.W., 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecol. Appl. 12(6), 1688-1701.

Black, C.C., 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. Adv. Ecol. Res. 7, 87-114.

Brye, K.R., Norman, J.M., Bundy, L.G.,Gower, S.T., 2000. Water-budget evaluation of prairie and maize ecosystems. Soil Sci. Soc. Am. J. 64(2), 715-724.

Brye, K.R.,Pirani, A.L., 2005. Native soil quality and the effects of tillage in the grand prairie region of eastern Arkansas. Am. Midl. Nat. 154(1), 28-41.

Burkart, M.R., Oberle, S.L., Hewitt, M.J.,Pickus, J., 1994. A framework for regional agroecosystems characterization using the national resources inventory. J. Environ. Qual. 23(5), 866-874.

Fay, P.A., Carlisle, J.D., Danner, B.T., Lett, M.S., McCarron, J.K., Stewart, C., Knapp, A.K., Blair, J.M.,Collins, S.L., 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. Int. J. Plant Sci. 163(4), 549-557.

Ghadiri, H., Rose, C.W.,Hogarth, W.L., 2001. The influence of grass and porous barrier strips on runoff hydrology and sediment transport. Trans. ASAE. 44(2), 259-268.

Groisman, P.Y., Knight, R.W.,Karl, T.R., 2012. Changes in intense precipitation over the Central United States. J. Hydrol. 13(1), 47-66.

Guo, X.S., Sinclair, T.R.,Ray, J.D., 1998. Effect of drought history on recovery of transpiration, photosynthesis, and leaf area development in maize. Soil Crop Sci. Soc. Fla. Proc. 57, 83-87.

Guzman, J.G.,Al-Kaisi, M.M., 2011. Landscape position effect on selected soil physical properties of reconstructed prairies in southcentral Iowa. J. Soil Water Conserv. 66(3), 183-191.

Halfield, J., 2012. Agriculture in the Midwest. In: U.S. National Climate Assessment Midwest Technical Input Report. J. Winkler, J. Andresen, J. Hatfield, D. Bidwell, D. Brown, coordinators. http://glisa.msu.edu/docs/NCA/MTIT_Agriculture.pdf.

Helmers, M.J., Zhou, X., Asbjornsen, H., Kolka, R., Tomer, M.D.,Cruse, R.M., 2012. Sediment removal by prairie filter strips in row-cropped ephemeral watersheds. J. Environ. Qual. 41(5), 1531-1539.

Hernandez-Santana, V., Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R.,Tomer, M., 2013. Native prairie filter strips reduce runoff from hillslopes under annual row-crop systems in Iowa, USA. J. Hydrol. 477, 94-103.

Hura, T., Grzesiak, S., Hura, K., Grzesiak, M.,Rzepka, A., 2006. Differences in the physiological state between triticale and maize plants during drought stress and followed rehydration expressed by the leaf gas exchange and spectrofluorimetric methods. Acta Physiol. Plant. 28(5), 433-443.

Jastrow, J.D., 1987. Changes in soil aggregation associated with tallgrass prairie restoration. Am. J. Bot. 74(11), 1656-1664.

Kemp, P.R.,Williams, G.J., 1980. A physiological-basis for niche separation between *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4). Ecology. 61(4), 846-858.

Martin, C.E., Harris, F.S.,Norman, F.J., 1991. Ecophysiological response of C_3 forbs and C_4 grasses to drought and rain on a tallgrass prairie in Northeastern Kansas. Bot. Gazette. 152(3), 257-262.

Meyer, L.D., Dabney, S.M.,Harmon, W.C., 1995. Sediment-trapping efectivenes of stiff-grass hedges. Trans. ASAE. 38(3), 809-815.

Ode, D.J., Tieszen, L.L.,Lerman, J.C., 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology. 61(6), 1304-1311.

Perez-Suarez, M., Castellano, M.J., Kolka, R., Asbjornsen, H.,Helmers, M., 2014. Nitrogen and carbon dynamics in prairie vegetation strips across topographical gradients in mixed Central Iowa agroecosystems. Agr. Ecosyst. Environ. 188, 1-11.

Rice, C.W., Todd, T.C., Blair, J.M., Seastedt, T.R., Ramundo, R.A.,Wilson, G.W.T., 1998. Belowground biology and processes. In: A.K. Knapp, J.M. Briggs, D.C. Hartnett and S.L. Collins (Editors), Long-Term Ecological Research Network Series; Grassland dynamics: Long-term ecological research in tallgrass prairie, pp. 244-264.

Samson, F.,Knopf, F., 1994. Prairie Conservation in North-America. Bioscience. 44(6), 418-421.

Schilling, K.E.,Jacobson, P., 2010. Groundwater conditions under a reconstructed prairie chronosequence. Agr. Ecosyst. Environ. 135(1-2), 81-89.

Schilling, K.E., Jha, M.K., Zhang, Y.K., Gassman, P.W.,Wolter, C.F., 2008. Impact of land use and land cover change on the water balance of a large agricultural watershed: Historical effects and future directions. Water Resour. Res. 44.

Schlesinger, W.H.,Jasechko, S., 2014. Transpiration in the global water cycle. Agric. For. Meteorol. 189, 115-117.

Swemmer, A.M., Knapp, A.K.,Smith, M.D., 2006. Growth responses of two dominant C_4 grass species to altered water availability. Int. J. Plant Sci. 167(5), 1001-1010.

Todd, C.E.D., Harbor, J.M.,Tyner, B., 2006. Increasing magnitudes and frequencies of extreme precipitation events used for hydraulic analysis in the Midwest. J. Soil Water Conserv. 61(4), 179-185.

Turner, C.L., Kneisler, J.R.,Knapp, A.K., 1995. Comparative gas exchange and nitrogen responses of the dominant C_4 grass *Andropogon gerardii* and 5 C_3 forbs to fire and topographic position in tallgrass prairie during wet year. Int. J. Plant Sci. 156(2), 216-226.

Udawatta, R.R., Anderson, S.H., Gantzer, C.J.,Garrett, H.E., 2008. Influence of prairie restoration on CT-measured soil pore characteristics. J. Environ. Qual. 37(1), 219-228.

USDA. 2007. Census of Agriculture. www.agcensus.usda.gov

Villarini, G., Smith, J.A.,Vecchi, G.A., 2013. Changing frequency of heavy rainfall over the Central United States. J. Clim. 26(1), 351-357.

Wang, L., Zhang, T.,Ding, S., 2006. Effect of drought and rewatering on photosynthetic physioecological characteristics of soybean. Acta Ecol. Sinica. 26(7), 2073-2078.

Weaver, J.E., 1954. North American prairie. Johnsen Pub. , Lincoln, Neb., 348 p. pp.

Zhang, Y.K.,Schilling, K.E., 2006. Increasing streamflow and baseflow in Mississippi River since the 1940's: Effect of land use change. J. Hydrol. 324(1-4), 412-422.

Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R.,Tomer, M.D., 2010. Perennial filter srips reduce nitrate levels in soil and shallow groundwater after grassland-to-cropland conversion. J. Environ. Qual. 39(6), 2006-2015.

Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R., Tomer, M.D.,Cruse, R.M., 2014. Nutrient removal by prairie filter strips in agricultural landscapes. J. Soil Water Conserv. 69(1), 54-64.

CHAPTER 2: EVAPOTRANSPIRATION AND PLANT WATER USE IN A RECONSTRUCTED PRAIRIE VERSUS A CROP FIELD IN THE US MIDWEST

A paper to be submitted to *Ecohydrology*

Vilma S. Mateos-Remigio, Heidi Asbjornsen, Thomas J. Sauer, Julie M. Tarara, David Meek, Virginia Hernandez-Santana

Abstract

Evapotranspiration (*ET*) patterns in the Midwestern US have been modified by the conversion of the native tallgrass prairie vegetation to intensively managed rowcrop agricultural systems, which has contributed to increased baseflow and stormflow, and loss of sediment and nutrients into the region's streams. Incorporation of native prairie vegetation within crop fields has been proposed as a possible means of improving hydrologic regulation. To assess the potential impact of prairie plantings in crop fields on *ET*, we measured *ET* using a Bowen ratio energy balance measurement system during the growing season (May 1 – October 5) over two consecutive years (2007 and 2008) in a 5-year old restored prairie and a crop field (alternate corn and soybean) located in central Iowa. Additionally, whole-plant water use measurements were collected using sap flow techniques during the peak growing season of 2008 to compare water use patterns between two dominant prairie species, *Ratibida pinnata* (C_3 forb) and *Andropogon gerardii* (C_4 grass), and the C_4 crop *Zea mays*. Results showed that although total growing season *ET* did not differ significantly between sites, prairie *ET* was significantly higher than crop *ET* during the early growing season weeks of

2007 and 2008 and late in the season in 2008. Both prairie species exhibited similar cumulative water use. In addition, the two prairie species, but not *Z. mays,* sharply increased their sap flow rates following a heavy precipitation event. More studies with other species and under different soil water conditions should be conducted to extend our knowledge concerning the impact of prairie vegetation in improving hydrological processes in agricultural watersheds.

Introduction

Evapotranspiration (*ET*), one of the main components of the hydrologic cycle and responsible for returning approximately 60% of the precipitation that falls on the Earth's land surface back to the atmosphere (Oki and Kanae, 2006), is strongly influenced by land use change, as transforming vegetation cover modifies leaf area indices, rooting depths, canopy structure, and albedo, all of which have impacts on *ET* (Calder, 1993; De Roo *et al.*, 2001). The Midwestern US, once dominated by tallgrass prairies, has undergone dramatic changes in land use, and in some states such as Iowa, as much as 80% of the land area is dominated by two annual crops: corn (*Zea mays* L.) and soybean (*Glycine max* L.) (Burkart *et al.*, 1994).

This landscape scale conversion of perennial to annual vegetation has altered seasonal patterns of *ET* since annual crops have a shorter growing season and, consequently, the ground is bare and exposed for longer time periods in spring and fall (Hatfield *et al.*, 2007). Several studies have reported that annual *ET* in the Midwest has been reduced, whereas baseflow has increased (Zhang and Schilling, 2006; Schilling *et al.*, 2008; Tomer and Schilling, 2009; Villarini *et al.*, 2011, Hernandez-Santana *et al.*, 2013), which combined with reduced infiltration rates and increased surface runoff, has contributed to greater export of

nutrients and sediment into streams and rivers (Jaynes *et al.*, 1999; Renwick *et al.*, 2008), and expansion of hypoxic zones in the Gulf of Mexico (Alexander *et al.*, 2008; Rabalais *et al.*, 2010). Thus, removing water excess from the soil by promoting higher plant water use may be especially advantageous in Midwestern agricultural landscapes (Hernandez-Santana *et al*., 2013).

The incorporation of native perennial vegetation into crop fields is increasingly being proposed as a means of reducing some of these negative impacts of row crop agriculture (Dosskey *et al.*, 2002; Schulte *et al.*, 2006; Swinton *et al.*, 2007; Asbjornsen *et al.*, 2014) Characteristics of perennial vegetation that can directly enhance hydrologic flows and regulation relative to annual crops include a longer growing season (Schilling and Libra, 2003), higher leaf area index (*LAI*) (Le *et al.*, 2011) mainly at the beginning and ending of the growing season, deeper rooting depth (Weaver, 1954), and species adapted to climatic variability (Craine *et al.*, 2013). Another important ecohydrological consequence of incorporating native prairie vegetation into row crop agricultural fields is a potential increase in *ET* (Burba and Verma, 2005; Hickman *et al.*, 2010; Le *et al*., 2011), and consequently greater soil moisture storage capacity and reduced runoff (Le *et al*., 2011; Hernandez-Santana *et al*. 2013, Gutierrez-Lopez *et al.*, 2014). This is particularly important in the Midwest as increases in rainfall and prevalence of wetter conditions particularly early in the season are predicted for the region (Patricola and Cook, 2013), which amplifies the effects of hydrological regulation loss due to intensive agriculture.

Despite the recognition that differences in *ET* between crop fields and native prairie vegetation have a key impact on hydrologic processes, comparative field data are largely lacking. Several studies have estimated annual and growing season *ET* for prairies (Ham and

Knapp, 1998; Bremer and Ham, 1999; Burba and Verma, 2001; Meyers, 2001; Wever *et al.*, 2002) and crops (Hatfield and Prueger, 2004; Hatfield *et al*., 2007; Sauer *et al.*, 2007; Suyker and Verma, 2009; Hernandez-Ramirez *et al.*, 2010), but few have made simultaneous comparison for both prairie and crop vegetation. In one study, Brye *et al*. (2000) estimated seasonal and annual *ET* in a restored prairie and two corn fields that differed in their management (no-tillage and chisel plow) over a 2.5-year period. They did not find differences in annual and cumulative *ET* among sites over the measurement period; however, the restored prairie consistently showed higher *ET* during the spring. In another multiyear study, Burba and Verma (2005) compared annual *ET* in a native tallgrass prairie and a wheat field, and found that prairie *ET* was higher than wheat *ET* in a year without soil water limitation, while the converse occurred in a dry year. The paucity of research on comparative water use patterns by annual crops and native prairie systems underscore the need for further work.

Further, plant species can vary widely in their physiological adaptations related to water uptake, and hence, knowledge about individual species' water use patterns is also important for designing effective mixed annual-perennial cropping systems. Tallgrass prairie ecosystems are dominated by C_4 grasses and C_3 forbs (Fay *et al.*, 2003), which differ in their water requirements (Taiz and Zeiger, 1998), phenology (Ode *et al.*, 1980), and leaf (Fay *et al.*, 2002), and root morphology (Weaver, 1954). Given that native prairie species are being considered for their potential to remove water excess, understanding how patterns of water uptake vary not only among native species, but also with respect to crops, is critical for anticipating possible impacts of reintroducing perennial vegetation on the watershed hydrology. However, comparative field measurements of whole-plant water use for annual

crops and prairie species is scarce, since most studies have been conducted on single species under greenhouse or chamber conditions (e.g., prairie species: Ham *et al.*, 1995; Bremer *et al.*, 1996; corn: Gavloski *et al.*, 1992; Kjelgaard *et al.*, 1997; soybean: Senock and Ham, 1993, Tan and Buttery, 1995. Only one study on corn (Bethenod *et al.*, 2000) and one study on soybean (Sauer *et al*., 2007) were conducted in the field. More importantly, none of them assessed species' water use in terms of its contribution to regulate hydrological processes. This knowledge gap needs more research, as some stomatal conductance measurements suggest that prairie species respond rapidly to rainfall events that are preceded by periods of water stress (Martin *et al.*, 1991; Fay *et al*., 2002; Swemmer *et al.*, 2006). In contrast, stomatal conductance of *Z. mays* has shown full recovery after 2-6 days of rewatering depending on the length of the preceding stress period and the degree of stress experienced by the plants (Guo *et al.*, 1998; Hura *et al.*, 2006).

In this study, *ET* was measured in a restored prairie and crop field during the growing season over two consecutive years characterized by no water limitation. During one month of the peak growing season (July 31-August 28) of 2008, we also measured whole-plant water use in a C_4 crop (*Zea mays* L.) and in the two dominant prairie species: a C_3 forb (*Ratibida pinnata* (Vent.) Barnh) and a C_4 grass (*Andropogon gerardii* Vitman). The main objective was to quantify and compare water use patterns at both the stand and individual plant scales for a restored prairie ecosystem and crop field. Three hypotheses were tested: 1) total growing season *ET* for the prairie ecosystem would be higher due to its longer active growing season; 2) differences in *ET* would be greatest in the early and late growing season when prairie *ET* is controlled by C_3 species, which have higher water use rates than the mid-season dominant C_4 species, and because crops are absent, not fully established or already

senescing; and 3) total water use of *R. pinnata* would be higher than that of *A. gerardii* due to contrasting physiological traits. Finally, we also scaled plant water use to the stand level in *Z. mays* in order to validate the technique used to take whole-plant measurements.

Materials and Methods

Study site

The study was conducted at the Neal Smith National Wildlife Refuge (NSNWR), which is situated within the Walnut Creek watershed in central Iowa (Figure 1). Measurements were made in a 5-year-old reconstructed prairie and an adjacent field managed under an intensive no-till rotational soybean (2007)-corn system (2008). Soil is predominantly mesic Mollic Hapludalf (Ladoga silt loam and Gara Loam) (Soil Conservation Service, 1979). The climate is humid, continental, with an annual precipitation of about 874 mm (30-year average, Midwestern Regional Climate Center, MRCC) and highest monthly rainfall typically occurring in May and June (Schilling and Spooner, 2006).

Evapotranspiration and micrometeorological measurements

A Bowen ratio energy balance (BREB) measurement system was installed at each site to estimate *ET*. Each system consisted of an air temperature/relative humidity probe (Model HMP45C, Vaisala Inc., Woburn, Mass., USA) and a thermistor. Sensors were mounted in aspirated radiation shields with a vertical separation of 1.5 m following the design of Bland *et al.* (1996) as adapted by Sauer *et al.* (2002). Sensor heights were adjusted as plant canopies developed to maintain the lower sensor about 0.5 m above the canopy. The sensors were exchanged every 5 min and values were averaged every 30 min. Bowen ratio data were

screened using criteria following Perez *et al.* (1999). The Bowen ratio (β) which is defined as the ratio of sensible to latent heat flux ($H/\lambda E$) is calculated as:

$$\beta = \frac{(PC_p[t_l - t_u])}{\lambda\varepsilon(e_l - e_u)} \quad (1)$$

Where P is atmospheric pressure [kPa], C_p is the specific heat capacity of air at constant pressure 1004.67 J kg^{-1} K^{-1}), t_l and t_u are the potential temperatures [K] at the lower and upper positions, respectively; λ is the latent heat of vaporization for water (2.45x10^6 J kg^{-1}), ε is the ratio of the molecular weights of air and water (0.622), and e_l and e_u are the vapor pressures at the lower and upper positions [kPa]. Potential temperature is calculated from air temperature recorded by the thermistor:

$$t = T_a \left(\frac{P_o}{P}\right)^{\frac{R}{Cp}} \quad (2)$$

Where T_a is the air temperature [K], P_o is the standard reference atmospheric pressure [kPa], P is the actual atmospheric pressure measured with a barometer (Model PTB-101B, Vaisala Inc.) [kPa], and R is the gas constant (8.314 J K^{-1} mol^{-1}). The latent heat flux (λE) [W m^{-2}] is calculated as:

$$\lambda E = \frac{R_n - G}{1+\beta} \quad (3)$$

Where R_n is the net radiation [W m^{-2}] and G is the soil heat flux at the soil surface [W m^{-2}]. Net radiation was measured with a model Q*7 net radiometer (Radiation and Energy Balance Systems, Seattle, Wash. USA) positioned ~2 m above each canopy. Soil heat flux was measured with three heat flux plates (HFT1.1, Radiation and Energy Balance Systems) at a depth of 0.06 m. Plate values were corrected for heat storage in the 0 to 0.06-m soil layer (Sauer, 2002). The latent heat flux was converted to mm of water with the following equation:

$$ET = \frac{\lambda E}{\lambda} * 1800 \quad (4)$$

Where 1800 represents the time between measurements in seconds [s]. The amount of available energy utilized for *ET*, the evaporative fraction (*EF*) was calculated as:

$$EF = \frac{\lambda E}{R_n - G} \quad (5)$$

Other microclimate variables measured on-site were solar radiation (R_s, Model LI200SZ pyranometer, LI-COR Biosciences, Inc.), wind speed (u) and direction (Wind Sentry cup anemometer and vane, R.M. Young Co., Traverse City, Mich. USA), rainfall (Model 529 tipping bucket rain gage, Texas Electronics Inc., Dallas, TX. USA), and T_a and relative humidity (*RH*) within and above the plant canopy (HMP45C, Vaisala, Inc.). The *T/RH* probes were installed within radiation shields. Vapor pressure deficit (*D*) was calculated as an average of above-canopy and below canopy saturated (e_s) and actual vapor pressure (e_a). Soil water content (θ) was measured using two water content reflectometers (model CS615; Campbell Scientific, Inc.), one installed parallel to the soil surface at 3 cm ($\theta_{0\text{-}6\ cm}$) and one installed at an angle from 6-20 cm ($\theta_{6\text{-}20\ cm}$). From all the variables monitored, only precipitation was averaged from both sites. Reference meteorological data were obtained from MesoWest, NSW14 station and National Oceanic and Atmospheric Administration (NOAA), Des Moines, Iowa station. Long-term mean values were derived from data recorded by MRCC, Newton, Iowa station (41°42'N, 93°01'W; 287.1 m), located approximately 34 km from the NSNWR.

Because planting and harvesting activities prevented access to the crop field in the early spring and fall, BREB systems were installed 24 days (2007) and 13 days (2008) later than in the prairie and removed 14 days earlier in 2007. In order to make a reasonable comparison among sites, we calculated *ET* (ET_c) for the missed days in the crop field by

using two approaches. When all climatic variables were available, we used the single crop coefficient (K_c) approach of FAO-56 (Allen *et al.*, 1998):

$$ET_c = K_c * ET_o \quad (6)$$

Local K_c values for each crop were calculated from daily *ET* measured (ET_m) by Hernandez-Santana *et al*. (In prep.) in 2011 and 2012 for soybean and corn respectively.

$$K_c = \frac{ET_m}{ET_o} \quad (7)$$

Evapotranspiration reference (ET_o) was calculated using the FAO Penman-Monteith equation (Allen *et al*., 1998) with micrometeorological data collected at the same site where ET_m was measured:

$$ET_o = \frac{0.408\Delta(R_n - G) + \gamma \frac{900}{T+273.15} u_2 (e_S - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \quad (8)$$

Where Δ is the slope of the vapor pressure curve [kPa $^oC^{-1}$], γ is the psychrometric constant [kPa $^oC^{-1}$], and u_2 is wind speed at 2 m height [m s^{-1}]. See FAO-56 guidelines (Allen *et al*., 1998) for more details on variables and calculations.

Since K_c was needed to be calculated for the beginning of the growing season ($K_{c\text{-}ini}$) in 2007 and 2008 and the end of the growing season ($K_{c\text{-}end}$) in 2007, an average K_c for each respective period was estimated. We found in the soybean field $K_{c\text{-}ini}$ was 0.27 and K_c-$_{end}$ was 0.21; whereas $K_{c\text{-}ini}$ in the corn field was 0.40. These values were used in Equation 6 along with ET_o estimated from climatic data collected in micrometeorological towers near to our study site.

For eight days in 2007 (DOY 137-144), there were no climatic data available to calculate ET_o, and daily *ET* was gap-filled using an iterative interpolation technique (Hernandez-Ramirez *et al*., 2010):

$$ET_{gap-filled} = \frac{\sum_{i=1}^{n} \frac{v}{t_i^2}}{\sum_{i=1}^{n} \frac{1}{t_i^2}} \quad (9)$$

Where v is a series of neighbored data points, t_i is the lag time between the period of missing data to be gap filled and its n nearest neighbors in time (Hernandez-Ramirez *et al*., 2010). This method was also used to estimate missing daily *ET* in the prairie site when any of the environmental sensors failed temporarily.

Plant water use measurements

Plant water use during the peak growing season in 2008 was estimated by sap flow measurements using the stem heat balance (SHB) technique. The theory of the method and equations are described extensively elsewhere (e.g., Baker and van Bavel, 1987). Briefly, a known quantity of heat is applied to the plant stem and the contribution of xylem flow to the dissipation of that heat is used to compute water flow in the xylem stream. The energy balance is defined as:

$$Q = Q_v + Q_r + Q_f + S \quad (10)$$

Where Q is the energy supplied to the sap flow gauge, Q_v is the heat dissipated by vertical conduction, Q_r is the heat dissipated by radial conduction and Q_f is the heat dissipated by convection in the sap. All components of the energy balance are in watts [W]. The heat stored by the stem (S) is considered negligible in small-diameter and herbaceous stems (Senock and Ham, 1993). The Q is calculated using Ohm's Law:

$$Q = \frac{V^2}{R} \quad (11)$$

Where V is the voltage supplied and R is the resistance [ohms] of the gauge heater. Vertical conduction is computed from:

$$Q_v = \frac{K_{st} A}{d_z(\Delta T_2 - \Delta T_1)} \quad (12)$$

Where K_{st} is the thermal conductivity of the stem, typically taken as 0.54 W m^{-1} K^{-1} for herbaceous stems (Sakuratani, 1984); A is the stem cross-sectional area [m^2]; d_z is the vertical distance [m] between thermocouples (0.003 m for *R. pinnata* and *A. gerardii*; 0.005 m for *Z. mays* gauges); and ΔT_2 and ΔT_1 are the up- and down-stream temperature differences [°C]. Radial heat flux is calculated as:

$$Q_r = K_{sh} E \quad (13)$$

Where K_{sh} is the gauge conductance [W mV^{-1}], which operationally is calculated during a time of zero or near-zero flow, usually assumed to occur before dawn (Baker and Nieber, 1989; Sakuratani, 1984), and E is a thermopile output. We approximated K_{sh} for each gauge from the mean value of K_{sh} between 5:18 h to 5:54 h LST (Local Standard Time).

Rearranging Equation (10) and by substitution, the mass flow rate of xylem sap flow, F [g s^{-1}] can be calculated from the heat capacity of water (c_p; 4.186 J $g^{-1}C^{-1}$ at 15°C) and the difference in temperature of the xylem sap above and below the gauge heater (ΔT_1 and ΔT_2):

$$F = \frac{Q_f}{cp\frac{\Delta T_1 - \Delta T_2}{2}} \quad (14)$$

Heat balance sap flow gauges were constructed according to Senock and Ham (1993). Gauges designed for 3, 5, and 19-mm diameter stems were installed on five plants of each of the three study species. In *Z. mays*, gauges were positioned at the second internode above the roots once there was enough stem length to accommodate the gauges. As lower portions of *Z. mays* plants started to senesce during the last two weeks of the study, gauges were reinstalled at the third internode. Gauges on all three species were located 15 to 20 cm above the ground

to minimize errors induced by heat transfer from the soil (Weibel and Devos, 1994). Gauges were wrapped with closed-cell foam insulation (3 to 4 cm thick) and covered with aluminum foil to reduce errors due to radiation loading. Any leaves located on the stem segment below the gauges were removed and were not included when determining leaf area. Because these leaves represented <1% of total leaf area and were located in the most shaded portion of the plant canopy, we assume that their removal resulted in a negligible underestimation of whole-plant water use.

A constant power system was used to supply energy to the gauges daily between 5:00 h and 22:00 h CST, and the power was reduced at night to avoid overheating the stems. The electrical power was supplied by a deep cycle battery (12 V) recharged by a solar panel. Gauge signals were sampled every 60 s and averaged every 12 min by a data logger (CR-10X) and multiplexer (AM16/32) arrangement (Campbell Scientific, Inc., Logan, Utah, USA).

Sap flow measurements were recorded for all three study species simultaneously from July 31 to August 27, 2008 (DOY 213-240). Sensors were rotated to new individuals periodically (3 times during the measurement period) and sampled plants were harvested and brought to the laboratory, where total leaf area of each plant was measured on an area meter (LI 3100, LI-COR Bioscience, Inc., Lincoln, Nebr. USA), and used to calculate F on a leaf area basis (F_{leaf}) [g m^{-2}].

Validation of plant water use measurements

Measurements of mean cumulative F [g day^{-1}] were scaled to the stand level to derive daily transpiration (T) [mm] for *Z. mays* with the following equation:

$$T = F\,\rho_w 10^3 De 10^{-10} \quad (15)$$

Where ρ_w is the density of water [g cm^{-3}], De is plant density (73,482 plants ha^{-1}), and the multipliers are unit conversion factors. Daily T for the prairie using field measurements of LAI as the scalar for F was not feasible due to the high degree of physiological variation among species and functional groups (Turner *et al.*, 1995) and because LAI does not account for effects of shading on vertical gradients in microclimate and water use by subcanopy species.

Data analysis

Daily ET, precipitation and R_n were summed on a weekly basis, whereas volumetric θ and D were averaged on a weekly basis. Weekly and average ET differences among sites for the complete growing season were analyzed using the Mann-Whitney rank sum test. Sap flow measurements were aggregated into four 1-week subperiods, as follows: July 31-August 3 (DOY 213-216), August 5-10 (DOY 218-223), August 12-19 (DOY 225-232) and August 21-27 (DOY 234-240), hereafter referred to as 'Week 1', 'Week 2', and so forth. Hourly and daily cumulative F_{leaf} were calculated between 7:00 h to 19:00 h LST. The trend in differences between paired observations of daily and cumulative F_{leaf} between species for each week and over the entire measurement period were modeled with simple parametric functions using nonlinear regression procedures (Meek *et al.*, 2001). Differences for each paired comparison were determined when the 95% confidence interval about the trend excluded zero.

Results

Annual and growing season microclimatic conditions

Mean annual temperature in 2007 was similar to the 30-year average, whereas in 2008 it was 19% lower (Figure 2a). Mean temperatures during the growing season in both 2007 and 2008 were similar to that of the long-term mean. Annual rainfall in 2007 (1056 mm) and 2008 (1197 mm) were 20% and 37% above the 30-year average, respectively (Figure 2b), while during the growing season total rainfall was 14% and 53% higher, respectively.

Microclimatic variables on a weekly basis over a 23-week period (May 1 - October 5) are shown in Figure 3. In 2007, precipitation occurrence was more concentrated in the second half of the growing season (Figure 3a), whereas in 2008 rainfall events were recorded in all weeks except for week 23 (Figure 3e). Figure 3b and 3f show that $\theta_{0\text{-}6\ cm}$ was always lower in the prairie site than in the crop field, but $\theta_{6\text{-}20\ cm}$ was quite similar between sites. Interestingly, crop $\theta_{0\text{-}6\ cm}$ was almost as high as $\theta_{6\text{-}20\ cm}$ in both prairie and crop site in 2008 (Figure 3f). Overall, $\theta_{6\text{-}20\ cm}$ was maintained above 0.3 in both sites and years in all weeks. Net radiation, which was closely tracked by *D,* exhibited different patterns among years. In 2007 (Figure 3c for R_n and 3d for D), both variables showed an increasing trend toward the peak of the growing season and declined after week 11, whereas in 2008 the increasing trend was not observed (Figure 3g and 3h for R_n and *D,* respectively) and they started to decrease 5 weeks later compared to 2007.

Growing season *ET* and *EF*

Measured and estimated *ET* and *EF* are presented in Figure 4a (2007) and 4b (2008). Weekly *ET* exhibited more or less a typical bell shaped distribution, which was less marked in 2008. Prairie *ET* was consistently higher than crop *ET* early (week 2 to 9 in 2007 and week 1 to 8 in 2008) and late (week 21 to 23 in both years) in the growing season. Significant differences between sites ($p < 0.05$) were found in weeks 3, 6 and 7, 11 and 15 in 2007, and in weeks 3, 21, 22 and 23 in 2008.

Average *ET* over the 23-week period did not show significant differences between sites, but still total prairie *ET* was 23.9 and 36.7 mm higher than the crop in 2007 and 2008, respectively (Table 1). However, prairie vegetation contribution to water removal (*ET/P*) was only 4% higher than the crop.

Mean weekly *EF* for prairie and crop over the growing season was 0.62 and 0.75, respectively, in 2007, and 0.72 and 0.64 in 2008. In general, *EF* followed the *ET* pattern in both years. Prairie had higher *EF* than crops early and late in the growing season when its *ET* was also higher. For the weeks when crop *ET* was higher than prairie in 2007, crop *EF* was also consistently higher. In contrast, *EF* was fairly similar at both sites in 2008, which reflected the lack of differences in *ET*.

Water use for individual species

Cumulative daily F_{leaf} over the peak growing season in 2008 varied between species, although total cumulative F_{leaf} at the end of the measurement period was similar for *R. pinnata* and *A. gerardii,* with 57.5 kg m^{-2} and 57.4 kg m^{-2}, respectively, and lower for *Z. mays* with 24.5 kg m^2 (Figure 5a). Cumulative F_{leaf} for *A. gerardii* was greater than for *Z.*

mays after DOY 218 (Week 2, Figure 5b), while *R. pinnata* had greater cumulative F_{leaf} than *Z. mays* for the entire measurement period (Figure 5c). Comparing the two prairie species, *R. pinnata* maintained greater cumulative F_{leaf} than *A. gerardii* for most of the measurement period, with the exception of Week 4, at which point the two species' cumulative F_{leaf} were not significantly different (Figure 5d).

Hourly F_{leaf}, precipitation, and θ, are shown in Figure 6. From all the rain events recorded during the study period (Figure 6a), rainfall amount was greatest on DOY 225 (27.2 mm). Hourly $\theta_{0\text{-}6\ cm}$ was always higher in the soil where *Z. mays* was grown (Figure 6b) compared to the prairie soil (Figure 6c-d), and the daily decline in $\theta_{0\text{-}6\ cm}$ at four weeks of measurements was steeper in the prairie. Hourly θ at both depths in the crop site was fairly similar, and with the rain event occurring on DOY 225, $\theta_{0\text{-}6\ cm}$ became somewhat higher than $\theta_{6\text{-}20\ cm}$ for 5 days (DOY 225-229). In contrast, hourly $\theta_{0\text{-}6\ cm}$ was permanently lower than $\theta_{6\text{-}20\ cm}$ in the prairie site.

Zea mays maintained nearly constant daily maximum F_{leaf} across the measurement period with a low degree of responsiveness to the DOY 225 rain event (Figure 6b). In contrast, daily F_{leaf} in *R. pinnata* decreased during Weeks 1 and 2 in the absence of rain, and then sharply increased following the DOY 225 rain event (Figure 6c). Patterns of F_{leaf} for *A. gerardii* were more constant during Weeks 1 and 2, but it also increased following the DOY 225 rain event in Week 3 (Figure 6d). The degree of increase in total daily F_{leaf} the day after the DOY 225 rain event (DOY 226) relative to the previous day (DOY 223) was approximately 203% in *R. pinnata*, 148% in *A. gerardii*, and 74% in *Z. mays*.

Validation of plant water use measurements

Daily *ET* data were compared with *T* data for *Z. mays* (excluding rainy days) to provide an independent measure of vegetation water use and assessment of the accuracy of sap flow measurements (Figure 7). Results revealed consistently higher *ET* compared to *T*, except on DOY 216, 218, 222 and 226. Cumulative crop *ET* during the measurement period was on average 11% higher than *T*.

Discussion

Comparison of prairie and crop *ET*

Total growing season *ET* estimated in this study (403.0 and 413.4 mm in prairie and 379.1 and 376.7 mm in crop in 2007 and 2008, respectively) are comparable with values reported by previous studies. Bremer and Ham (1999) reported *ET* values of 503 mm and 408 mm for burned and unburned tallgrass prairie at the Konza Prairie Biological Station from data collected during April 19-September 15, 1997. Burba and Verma (2005) found that growing season *ET* (May - October) for a tallgrass prairie ranged from 480 mm to 607.5 mm in a multiple year-study conducted in Oklahoma. Suyker and Verma (2009) found *ET* from planting to harvesting in an irrigated crop field in Nebraska managed by corn-soybean rotation was 474 and 430 mm in soybean years, and 535, 578 and 550 mm in corn years.

Contrary to what was hypothesized, total *ET* in the restored prairie was similar to total crop *ET* over a 23-weeks period (May 1 - October 5) in 2007 and 2008 regardless of the difference in precipitation between years. Nonetheless, our second hypothesis was confirmed as significantly higher prairie *ET* was found intermittently in May and June (2007) compared to soybean *ET*; whereas in 2008, prairie *ET* was higher than corn *ET* during one week in May

(week 3) and the last days of September and first days of October (weeks 21, 22 and 23). The lack of difference in total *ET* among prairie and crops is not entirely new. Brye *et al.* (2000) did not find differences in cumulative *ET* for a corn field and a restored prairie. However, similar to our study, they found that the prairie site started and finished transpiring 5-6 weeks earlier and 2-3 weeks later, respectively, than the corn field. These findings lend support to the potential for prairie vegetation to improve hydrological regulation early and late in the season when occurrence of precipitation events could result in runoff and flooding.

Results found in our study may be attributed to differences in rooting depth and *LAI* among sites, as well as to the phenology and physiology of the species. For example, despite the relatively low or lack of precipitation and the consequent decline in prairie $\theta_{0\text{-}6\ cm}$ during weeks 2, 3 and 6 in 2007, prairie *ET* exhibited an upward trend. In contrast, the decrease in crop $\theta_{0\text{-}6\ cm}$ was associated with a sharp decrease in crop *ET* mainly in weeks 6 and 7, as well as an abrupt reduction in *EF* when only a small fraction of available energy (0.27 and 0.29) was used as λE. The reduction in both *ET* and *EF* at the crop site may be explained by the age of the plants. Soybean plants were approximately two weeks old by week 6, so that roots were not long enough to reach water from below 6 cm in the soil. On the contrary, prairie *ET* was sustained by perennial C_3 species that show high stomatal conductance rates to water vapor (Turner *et al*., 1995), and also have better developed roots (Weaver, 1954) and are able to take water from deeper soil layers (Nippert and Knapp, 2007; Nippert *et al.*, 2012). In the last weeks of the growing season in 2008, the significantly higher prairie *ET* might also be explained by the presence of C_3 species that become active early in the fall as temperature decreases (Ode *et al*., 1980; Craine *et al.*, 2012), while in the crop site, all plants had started to senesce.

Although *LAI* was not consistently measured over the growing season in both years, its effect on *ET* was observed in the middle of the growing season. Leaf area index measurements taken on July 17 (week 12), 31 (week 14) and August 17 (week 16) in 2007 showed that crop *LAI* was 3.4, 5.4 and 5.5 compared to 3.2, 4.5 and 4.9 in prairie, respectively. These differences may explain the relatively higher *ET* and *EF* measured in the crop site during the peak growing season. Additionally, prairie species composition may also have contributed to the differences observed between sites. From the middle of June to the middle of August, approximately weeks 7-15 in our study, prairie vegetation is dominated by C_4 species (Ode *et al*., 1980), which have lower rates of water consumption than C_3 species (Turner *et al*., 1995). Since the crop grown in 2007 (soybean) was a C_3, it seems logical that crop *ET* would be higher than prairie *ET*, even though differences between sites were not significant except for weeks 11 and 15. The results from 2008 comparing corn and prairie are also consistent with this interpretation, as *ET* and *EF* between sites from week 9 to 18 were more similar, possibly reflecting the dominance of C_4 species at both sites.

Overall, weekly *ET* did not respond to precipitation events at either site, not even to the heavy precipitation events recorded in weeks 9 and 12 in 2008, which occurred after a week of low precipitation. This result contrasts with the 10-day *ET* reported by Meyers (2001), who found that in a dry year, a rangeland dominated by little bluestem (*Schizachyrium scoparium* (Michx.) Nash) in southwest Oklahoma responded to minor precipitation events occurring in August by increasing ET. However, our sites never experienced soil water limitation at depths below 6 cm and this may largely explain the lack of *ET* response to rainfall events. In the absence of soil moisture limitation, *ET* is mainly driven by changes in green leaf area index (Burba and Verma, 2005) and R_n (Li *et al.*, 2005;

Mackay *et al.*, 2007). In our study, weekly *ET* patterns were closely coupled to weekly R_n changes, as confirmed by correlation analysis (not shown) where coefficients ranged from 0.7 (crop) to 0.9 (prairie) for both years.

Comparison of plant water use

An interesting finding from this study is that cumulative F_{leaf} was similar for both the C_3 and C_4 prairie species during an exceptionally wet year, which does not support our hypothesis of higher water use for the C_3 species. Native prairie species often exhibit rapid ecophysiological adjustments in their rates of photosynthesis and stomatal conductance in response to changes in moisture availability (Knapp, 1984; Silletti and Knapp, 2001; Nippert *et al.*, 2009). Under conditions of relatively low plant moisture stress, as in our study, differences in water use patterns between C_3 and C_4 species may have been dampened, potentially contributing to the similar four-week cumulative F_{leaf} among the two prairie species. Although comparative field data for F_{leaf} are not available, instantaneous measurements of stomatal conductance provide supporting evidence that differences among functional groups may be less pronounced when water availability is not limiting (i.e. Turner *et al*., 1995; Thurman and Martin, 2000; Nippert *et al.*, 2007).

Differences in daily F_{leaf} for the two prairie species reported in this study may in part be explained by inherent physiological and phenological differences between the two functional groups as well as changes in canopy position. The consistently higher F_{leaf} in *R. pinnata* than *A. gerardii* in late July and early August (Week 1) agrees with the typically higher water requirement and lower *WUE* of C_3 species (Knapp, 1993). During the latter half

of August, *A. gerardii's* F_{leaf} became taller as this species assumed a dominant canopy position and *R. pinnata* experienced greater shading in the mid-canopy.

Particularly noteworthy in this study was that whole prairie plants exhibited a greater water use response to heavy precipitation input than crop plants during the 2008 peak growing season. We are not aware of any studies that have conducted field measurements of whole-plant sap flow response to precipitation events for prairie or crop species, but gas exchange measurements provide useful comparative data for discussing general patterns. Thus, F_{leaf} response in this study is consistent with Martin *et al.'s* (1991) who found significant increases in stomatal conductance after a rain event that followed a severe drought in seven tallgrass prairie C_3 forb species and two C_4 grasses (*A. gerardii* and *A. scoparius*). Similarly, Swemmer *et al*. (2006) observed a rapid and significant recovery in *A. gerardii's* stomatal conductance after plants were rewatered once they had wilted. Fay *et al*. (2002) also reported a positive relationship between stomatal conductance and soil moisture for the C_3 forb *Solidago canadensis*, but not for the C_4 grass *A. gerardii*. Later, Nippert *et al*. (2009) found contrasting results for *A. gerardii* and another C_4 grass (*Sorghastrum nutans* (L.) Nash). In the first year of their study, both species showed a decline in stomatal conductance after being rewatered, while in the second year both species responded positively.

We suggest that the dissimilar response between prairie species with respect to the crop is due to dissimilar conditions of $\theta_{0\text{-}6\ cm}$ between sites, which in turn might be related to the difference in water use rates between prairie species and *Z. mays*. In this study we showed that F_{leaf} rates were usually higher in the prairie species than in the crop. Mateos *et al.* (unpublished data) found that stomatal conductance was always higher in the C_3 *S. canadensis*, followed by *A. gerardii* and lowest for *Z. mays*. Thus, higher water use rates in

the prairie site together with an absence of soil water recharge in Weeks 1 and 2, caused a fast and substantial depletion of water mainly in the upper 0-6 cm soil layer. In response, F_{leaf} in both prairie species started to decline (DOY 221-223) prior to the rainfall on DOY 225. It is known that there is an asymptotic relationship between stomatal conductance and extractable soil water content (Turner, 1991) and it explains the sharp increase in F_{leaf} following the soil water recharge that occurred after the DOY 225 rainfall event. Unlike the prairie species, *Z. mays'* F_{leaf} did not respond to rainfall, likely because θ remained fairly stable during the measurements period (above 0.3) so that plants did not experience water deficit. Based on the few studies that have evaluated stomatal conductance or transpiration recovery after water deficit in maize (Beardsell and Cohen, 1975; Guo *et al*., 1998), it is likely that *Z. mays* might have also responded to the precipitation event if it had experienced water stress.

Validation of individual water use measurements

Overall, our field measurements of sap flow fall within the broader range of measurements for similar species reported in the literature. Maximum hourly *F* in *Z. mays* (120 g h^{-1}) was slightly below the range reported by Peressotti and Ham (1996) and Kjelgaard *et al*. (1997) of 140 to 150 g h^{-1}, also using the SHB method. Maximum hourly *F* in *A. gerardii* (4.5 g h^{-1}) was slightly higher than the maximum rate of 4 g h^{-1} reported by Senock and Ham (1995) for *A. gerardii* in the laboratory. For *A. gerardii,* the maximum hourly (484 g h^{-1} m^{-2}) and daily (3,321 g m^{-2}) F_{leaf} values recorded in our study were similar to values reported by Bremer *et al.* (1996) for *A. gerardii* under field conditions (400-450 g h^{-1} m^{-2} and 3,000 g m^{-2} for hourly and daily F_{leaf} respectively). We are aware of no previous

studies quantifying transpiration in *R. pinnata*, but maximum hourly F_{leaf} obtained in our study (500 g h^{-1} m^{-2}) was higher than rates reported for another C_3 forb, *Vernonia baldwinii* Torr. (nearly 300 g h^{-1} m^{-2}) under field conditions (Bremer *et al*., 1996).

As expected, daily crop *ET* was generally higher than daily *T*, because the former includes contributions by soil water and dew evaporation. The few days (DOY 216, 218, 222 and 226) when daily *T* exceeded *ET* may be explained by two factors acting individually or together. Higher *T* than *ET* on DOY's 218 and 226 were preceded by rainfall, and then SHB gauges were probably wet. We have observed noisy data when gauges become wet, which could have overestimated F_{leaf} and consequently *T*. In addition, overestimations of *F* at mid-day, when maximum sap flow occurs, might have contributed to higher *T* on DOY's 216, 222 and 226. Studies conducted by Ham and Heilman (1990), Cohen *et al*. (1993) and Kjelgaard *et al*. (1997), for example, have also reported overestimations at flow rates above 100 g h^{-1}, and they have attributed the error to the temperature imbalance between the xylem and surface of the stem. However, the difference of almost 1mm in *T* with respect to *ET* on DOY 216 is still difficult to explain only by mid-day *F* overestimation, although no other possible sources of error were found.

In general, the average difference in $ET - T$ (11%) found in our study was likely due to additional contributions by soil evaporation to *ET*. This explanation is consistent with results reported by Bethenod *et al*. (2000). They measured *ET* in a *Z. mays* field ($LAI \sim 4.0$) using both SHB and BREB techniques and similarly attributed the 10-12% lower *T* than *ET* to soil water evaporation.

Implications for watershed hydrology

Our hypothesis that reconstructed prairie would have higher total growing season *ET* than annual crop fields was not supported by our results during two years with no water limitation. However, our findings showing greater *ET* by prairie vegetation during the early and late parts of the growing season suggest that planting prairie vegetation within crop fields might help to reduce the negative impact of wet springs, when crop fields are still bare and the risk for high runoff and nutrient and sediment loss is particularly high.

Interestingly, $\theta_{0\text{-}6\ cm}$ was always lower in the prairie site than in the crop. Previous studies have shown higher θ in crops fields compared to areas covered by perennial vegetation. Tufekcioglu *et al*. (2001) found that θ in the 0-5 cm depth was always significantly higher under crop fields (corn and soybean) compared to cool season grass and switchgrass strips. Similarly, Wang *et al*. (2013) reported that mean θ in the 1m-soil profile was lower in a field covered by grass (*Andropogon sp*.) than in a corn field. As a result, lower θ in the upper layer of the soil would provide the prairie ecosystems a higher capacity to capture more water when heavy rainfall events occur, and consequently, to reduce surface runoff. Additionally, it has been shown that perennial species improve soil physical characteristics (e.g., porosity, soil organic carbon, bulk density) and infiltration (Marquez *et al.*, 1998; Bharati *et al.*, 2002; Udawatta *et al.*, 2008; Anderson *et al.*, 2009; Guzman and Al-Kaisi, 2011), which all together increase the benefits provided by perennial vegetation in terms of hydrologic regulation.

Conclusions

In this study, measurements of growing season *ET* and whole-plant water use in a restored prairie and a crop field were used to assess the potential contribution of native perennial vegetation in enhancing hydrologic functions in an agriculturally dominated region, especially during wet years. Total growing season (May 1 - October 5) *ET* was similar between a restored prairie and a crop field. Thus, the perennial vegetation did not show any advantage over the crop plants in any year of study. Still perennial species showed higher *ET* early in the season of 2007 and late in the season of 2008, as hypothesized. In addition, water use measurements at the whole-plant level during the peak growing season of 2008 showed that perennial species have higher responsiveness than the crop species (*Z. mays*) to water inputs. These measurements also showed that the C_4 grass was able to increase its water use rates such that there was no difference in the cumulative water use relative to the C_3 forb.

Although soil evaporation was not measured simultaneously with sap flow, the residual of corn *ET* minus *T* (11%) suggests that sap flow measurements obtained using the SHB technique in this study provide reasonable estimates of whole-plant water use.

Future work should focus on assessing seasonal and annual water use dynamics among a broader range of crop and prairie species, and whole fields and ecosystems over longer time periods (including the early growing season when prairie is active but annual crops have not yet established) and under contrasting climatic conditions (e.g., ideally comparing high versus low rainfall years or conducting rainfall simulation experiments).

Acknowledgements

Funding for this research was provided by the Leopold Center for Sustainable Agriculture, Iowa State University's College of Agriculture and Life Sciences, USDA Forest Service Northern Research Station, Iowa Department of Agriculture and Land Stewarship, USDA North Central Region SARE Program, USDA-AFRI Managed Ecosystem Program and the NSF Biocomplexity in the Environment Program (Grant NSF BE/CNH Award #0508091). The authors thank David Williams, Tim Hart, Forrest Goodman and Agustina Sanchez-Parada for their technical and field assistance.

References

Alexander RB, Smith RA, Schwarz GE, Boyer EW, Nolan JV, Brakebill JW. 2008. Differences in phosphorus and nitrogen delivery to the gulf of Mexico from the Mississippi river basin. *Environmental Science and Technology* **42**: 822-830. doi:10.1021/es0716103

Allen R, Pereira LS, Raes D, Smith M 1998. *Crop evapotranspiration: Guidelines for computing crop water requirements.* United Nations FAO: Rome.

Anderson SH, Udawatta RP, Seobi T, Garrett HE. 2009. Soil water content and infiltration in agroforestry buffer strips. *Agroforestry Systems* **75**: 5-16. doi:10.1007/s10457-008-9128-3

Asbjornsen H, Hernandez-Santana V, Liebman M, Bayala J, Chen J, Helmers M, Ong CK, Schulte LA. 2014. Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. *Renewable Agriculture and Food Systems* **29**: 101-125. doi:10.1017/s1742170512000385

Baker JM, Nieber JL. 1989. An analysis of the steady state heat balance method for measuring sap flow in plants. *Agricultural and Forest Meteorology* **48**: 93-109.

Baker JM, van Bavel CHM. 1987. Measurement of mass flow of water in the stems of herbaceous plants. *Plant Cell and Environment* **10**: 777-782.

Beardsell MF, Cohen D. 1975. Relationships between leaf area status, abscisic acid levels, and stomatal resistance in maize and sorghum. *Plant Physiology* **56**: 207-212. doi:10.1104/pp.56.2.207

Bethenod O, Katerji N, Goujet R, Bertolini JM, Rana G. 2000. Determination and validation of corn crop transpiration by sap flow measurement under field conditions. *Theoretical and Applied Climatology* **67**: 153-160.

Bharati L, Lee KH, Isenhart TM, Schultz RC. 2002. Soil-water infiltration under crops, pasture, and established riparian buffer in Midwestern USA. *Agroforestry Systems* **56**: 249-257. doi:10.1023/a:1021344807285

Bland WL, Loew JT, Norman JM. 1996. Evaporation from cranberry. *Agricultural and Forest Meteorology* **81**: 1-12.

Bremer DJ, Ham JM. 1999. Effect of spring burning on the surface energy balance in a tallgrass prairie. *Agricultural and Forest Meteorology* **97**: 43-54.

Bremer DJ, Ham JM, Owensby CE. 1996. Effect of elevated atmospheric carbon dioxide and open-top chambers on transpiration in a tallgrass prairie. *Journal of Environmental Quality* **25**: 691-701.

Brye KR, Norman JM, Bundy LG, Gower ST. 2000. Water-budget evaluation of prairie and maize ecosystems. *Soil Science Society of America Journal* **64**: 715-724.

Burba GG, Verma SB. 2001. Prairie growth, PAR albedo and seasonal distribution of energy fluxes. *Agricultural and Forest Meteorology* **107**: 227-240. doi:Doi 10.1016/S0168-1923(00)00233-1

Burba GG, Verma SB. 2005. Seasonal and interannual variability in evapotranspiration of native tallgrass prairie and cultivated wheat ecosystems. *Agricultural and Forest Meteorology* **135**: 190-201. doi:10.1016/j.agrformet.2005.11.017

Burkart MR, Oberle SL, Hewitt MJ, Pickus J. 1994. A framework for regional agroecosystems characterization using the national resources inventory. *Journal of Environmental Quality* **23**: 866-874.

Calder IR. 1993. Hydrologic effects of land-use change, In: DR Maidment (Ed.), *Handbook of hydrology.* McGraw-Hill. New York. 50

Cohen Y, Takeuchi S, Nozaka J, Yano T. 1993. Accuracy of sap flow measurement using heat balance and heat pulse methods. *Agronomy Journal* **85**: 1080-1086.

Craine JM, Ocheltree TW, Nippert JB, Towne EG, Skibbe AM, Kembel SW, Fargione JE. 2013. Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change* **3**: 63-67. doi:10.1038/nclimate1634

Craine JM, Wolkovich EM, Towne EG, Kembel SW. 2012. Flowering phenology as a functional trait in a tallgrass prairie. *New Phytologist* **193**: 673-682. doi:10.1111/j.1469-8137.2011.03953.x

De Roo A, Odijk M, Schmuck G, Koster E, Lucieer A. 2001. Assessing the effects of land use changes on floods in the Meuse and Oder catchment. *Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere* **26**: 593-599. doi:10.1016/s1464-1909(01)00054-5

Dosskey MG, Helmers MJ, Eisenhauer DE, Franti TG, Hoagland KD. 2002. Assessment of concentrated flow through riparian buffers. *Journal of Soil and Water Conservation* **57**: 336-343.

Fay PA, Carlisle JD, Danner BT, Lett MS, McCarron JK, Stewart C, Knapp AK, Blair JM, Collins SL. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences* **163**: 549-557.

Fay PA, Knapp AK, Blair JM, Carlisle JD, Danner BT, Mccarron JK. 2003. Rainfall timing, soil moisture dynamics, and plant response in a mesic tallgrass prairie ecosystem, In: JF Weltzin and GR McPherson (Ed.), *Changing precipitation regimes and terrestrial ecosystems.* The University of Arizona Press. USA. 147-163.

Gavloski JE, Whitfield GH, Ellis CR. 1992. Effect of restricted watering on sap flow and growth in corn (*Zea mays* L.). *Canadian Journal of Plant Science* **72**: 361-368.

Guo XS, Sinclair TR, Ray JD. 1998. Effect of drought history on recovery of transpiration, photosynthesis, and leaf area development in maize. *Soil and Crop Science Society of Florida Proceedings* **57**: 83-87.

Gutierrez-Lopez J, Asbjomsen H, Helmers M, Isenhart T. 2014. Regulation of soil moisture dynamics in agricultural fields using strips of native prairie vegetation. *Geoderma* **226**: 238-249. doi:10.1016/j.geoderma.2014.02.013

Guzman JG, Al-Kaisi MM. 2011. Landscape position effect on selected soil physical properties of reconstructed prairies in southcentral Iowa. *Journal of Soil and Water Conservation* **66**: 183-191. doi:10.2489/jswc.66.3.183

Ham JM, Heilman JL. 1990. Dynamics of a heat balance stem flow gauge during high flow. *Agronomy Journal* **82**: 147-152.

Ham JM, Knapp AK. 1998. Fluxes of CO_2 water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. *Agricultural and Forest Meteorology* **89**: 1-14. doi:Doi 10.1016/S0168-1923(97)00062-2

Ham JM, Owensby CE, Coyne PI, Bremer DJ. 1995. Fluxes of CO_2 and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO_2. *Agricultural and Forest Meteorology* **77**: 73-93. doi:10.1016/0168-1923(95)02230-u

Hatfield JL, Prueger JH. 2004. Impacts of changing precipitation patterns on water quality. *Journal of Soil and Water Conservation* **59**: 51-58.

Hatfield JL, Prueger JH, Kustas WR. 2007. Spatial and temporal variation of energy and carbon fluxes in central Iowa. *Agronomy Journal* **99**: 285-296. doi:10.2134/agronj2005.0116S

Hernandez-Ramirez G, Hatfield JL, Prueger JH, Sauer TJ. 2010. Energy balance and turbulent flux partitioning in a corn-soybean rotation in the Midwestern US. *Theoretical and Applied Climatology* **100**: 79-92. doi:DOI 10.1007/s00704-009-0169-y

Hernandez-Santana V, Zhou X, Helmers MJ, Asbjornsen H, Kolka R, Tomer M. 2013. Native prairie filter strips reduce runoff from hillslopes under annual row-crop systems in Iowa, USA. *Journal of Hydrology* **477**: 94-103. doi:10.1016/j.jhydrol.2012.11.013

Hickman GC, Vanloocke A, Dohleman FG, Bernacchi CJ. 2010. A comparison of canopy evapotranspiration for maize and two perennial grasses identified as potential bioenergy crops. *Global Change Biology Bioenergy* **2**: 157-168. doi:10.1111/j.1757-1707.2010.01050.x

Hura T, Grzesiak S, Hura K, Grzesiak M, Rzepka A. 2006. Differences in the physiological state between triticale and maize plants during drought stress and followed rehydration expressed by the leaf gas exchange and spectrofluorimetric methods. *Acta Physiologiae Plantarum* **28**: 433-443. doi:10.1007/bf02706626

Jaynes DB, Hatfield JL, Meek DW. 1999. Water quality in Walnut Creek watershed: Herbicides and nitrate in surface waters. *Journal of Environmental Quality* **28**: 45-59.

Kjelgaard JF, Stockle CO, Black RA, Campbell GS. 1997. Measuring sap flow with the heat balance approach using constant and variable heat inputs. *Agricultural and Forest Meteorology* **85**: 239-250.

Knapp AK. 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. *Oecologia* **65**: 35-43. doi:Doi 10.1007/Bf00384460

Knapp AK. 1993. Gas exchange dynamics in C_3 and C_4 grasses: consequences of differences in stomatal conductance. *Ecology* **74**: 113-123.

Le PVV, Kumar P, Drewry DT. 2011. Implications for the hydrologic cycle under climate change due to the expansion of bioenergy crops in the Midwestern United States. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 15085-15090. doi:10.1073/pnas.1107177108

Li SG, Lai CT, Lee G, Shimoda S, Yokoyama T, Higuchi A, Oikawa T. 2005. Evapotranspiration from a wet temperate grassland and its sensitivity to microenvironmental variables. *Hydrological Processes* **19**: 517-532. doi:10.1002/hyp.5673

Mackay DS, Ewers BE, Cook BD, Davis KJ. 2007. Environmental drivers of evapotranspiration in a shrub wetland and an upland forest in northern Wisconsin. *Water Resources Research* **43** doi:W0344210.1029/2006wr005149

Marquez CO, Cambardella CA, Isenhart TM, Schultz RC. 1998. Assessing soil quality in a riparian buffer by testing organic matter fractions in central Iowa, USA. *Agroforestry Systems* **44**: 133-140. doi:10.1023/a:1006261519080

Martin CE, Harris FS, Norman FJ. 1991. Ecophysiological response of C_3 forbs and C_4 grasses to drought and rain on a tallgrass prairie in Northeastern Kansas. *Botanical Gazette* **152**: 257-262.

Meek D, Dinnes D, Jaynes D, Cambardela C, Colvin T, Hatfield JL, Kerlen D. 2001. An autoregression model for a paired watershed comparison, In: G Milliken (Ed.), *Proceedings of 12th Applied Statistics in Agriculture Conference* Kansas State University.

Meyers TP. 2001. A comparison of summertime water and CO2 fluxes over rangeland for well watered and drought conditions. *Agricultural and Forest Meteorology* **106**: 205-214. doi:10.1016/s0168-1923(00)00213-6

Nippert JB, Fay PA, Carlisle JD, Knapp AK, Smith MD. 2009. Ecophysiological responses of two dominant grasses to altered temperature and precipitation regimes. *Acta Oecologica* **35**: 400-408. doi:10.1016/j.actao.2009.01.010

Nippert JB, Fay PA, Knapp AK. 2007. Photosynthetic traits in C_3 and C_4 grassland species in mesocosm and field environments. *Environmental and Experimental Botany* **60**: 412-420. doi:10.1016/j.envexpbot.2006.12.012

Nippert JB, Knapp AK. 2007. Linking water uptake with rooting patterns in grassland species. *Oecologia* **153**: 261-272. doi:10.1007/s00442-007-0745-8

Nippert JB, Wieme RA, Ocheltree TW, Craine JM. 2012. Root characteristics of C_4 grasses limit reliance on deep soil water in tallgrass prairie. *Plant and Soil* **355**: 385-394. doi:10.1007/s11104-011-1112-4

Ode DJ, Tieszen LL, Lerman JC. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. *Ecology* **61**: 1304-1311. doi:10.2307/1939038

Oki T, Kanae S. 2006. Global hydrological cycles and world water resources. *Science* **313**: 1068-1072. doi:10.1126/science.1128845

Patricola C, Cook K. 2013. Mid-twenty-first century warm season climate change in the Central United States. Part I: regional and global model predictions. *Climate Dynamics* **40**: 551-568. doi:10.1007/s00382-012-1605-8

Peressotti A, Ham JM. 1996. A dual-heater gauge for measuring sap flow with an improved heat-balance method. *Agronomy Journal* **88**: 149-155.

Perez PJ, Castellvi F, Ibanez M, Rosell JI. 1999. Assessment of reliability of Bowen ratio method for partitioning fluxes. *Agricultural and Forest Meteorology* **97**: 141-150.

Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J. 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* **7**: 585-619.

Renwick WH, Vanni MJ, Zhang Q, Patton J. 2008. Water quality trends and changing agricultural practices in a Midwest US watershed, 1994-2006. *Journal of Environmental Quality* **37**: 1862-1874. doi:10.2134/jeq2007.0401

Sakuratani T. 1984. Improvement of the probe for measuring water flow rate in intact plants with the stem heat balance method. *Journal of Agricultural Meteorology* **40**: 273-277.

Sauer TJ. 2002. Heat flux density, In: JD Dane and JC Topp (Ed.), *Methods of soil analysis - Part I, Physical and mineralogical methods.* American Society of Agronomy. Wisconsin. 1233-1248.

Sauer TJ, Moore PA, Ham JM, Bland WL, Prueger JH, West CP. 2002. Seasonal water balance of an Ozark hillslope. *Agricultural Water Management* **55**: 71-82.

Sauer TJ, Singer JW, Prueger JH, DeSutter TM, Hatfield JL. 2007. Radiation balance and evaporation partitioning in a narrow-row soybean canopy. *Agricultural and Forest Meteorology* **145**: 206-214. doi:DOI 10.1016/j.agrformet.2007.04.015

Schilling KE, Jha MK, Zhang YK, Gassman PW, Wolter CF. 2008. Impact of land use and land cover change on the water balance of a large agricultural watershed: Historical effects and future directions. *Water Resources Research* **44** doi:W00a0910.1029/2007wr006644

Schilling KE, Libra RD. 2003. Increased baseflow in Iowa over the second half of the 20th century. *Journal of the American Water Resources Association* **39**: 851-860. doi:10.1111/j.1752-1688.2003.tb04410.x

Schilling KE, Spooner J. 2006. Effects of watershed-scale land use change on stream nitrate concentrations. *Journal of Environmental Quality* **35**: 2132-2145. doi:10.2134/jeq2006.0157

Schulte LA, Liebman M, Asbjornsen H, Crow TR. 2006. Agroecosystem restoration through strategic integration of perennials. *Journal of Soil and Water Conservation* **61**: 164A-169A.

Senock RS, Ham JM. 1993. Heat balance sap flow gauge for small diameter stems. *Plant Cell and Environment* **16**: 593-601.

Senock RS, Ham JM. 1995. Measurements of water use by prairie grasses with heat balance sap flow gauges. *Journal of Range Management* **48**: 150-158.

Soil Conservation Service. 1979. Soil survey of Jasper county, Iowa. United States Department of Agriculture, Soil Conservation Service, Washington, D.C.

Silletti AM, Knapp AK. 2001. Responses of the codominant grassland species *Andropogon gerardii* and *Sorghastrum nutans* to long-term manipulations of nitrogen and water. *American Midland Naturalist* **145**: 159-167. doi:10.1674/0003-0031(2001)145[0159:rotcgs]2.0.co;2

Suyker AE, Verma SB. 2009. Evapotranspiration of irrigated and rainfed maize-soybean cropping systems. *Agricultural and Forest Meteorology* **149**: 443-452. doi:10.1016/j.agrformet.2008.09.010

Swemmer AM, Knapp AK, Smith MD. 2006. Growth responses of two dominant C_4 grass species to altered water availability. *International Journal of Plant Sciences* **167**: 1001-1010. doi:10.1086/505611

Swinton SM, Lupi F, Robertson GP, Hamilton SK. 2007. Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. *Ecological Economics* **64**: 245-252. doi:10.1016/j.ecolecon.2007.09.020

Taiz L, Zeiger E 1998. *Plant physiology.* Sinauer Associates: Sunderland, Mass.

Tan CS, Buttery BR. 1995. Determination of the water use of two pairs of soybean isolines difering in stomatal frequency using a heat balance stem flow gauge. *Canadian Journal of Plant Science* **75**: 99-103.

Thurman CM, Martin CE. 2000. Growth, leaf temperatures, and leaf conductances of C_3 forbs and C_4 grasses in a tallgrass prairie in northeastern Kansas, USA. *Flora* **195**: 25-34.

Tomer MD, Schilling KE. 2009. A simple approach to distinguish land-use and climate-change effects on watershed hydrology. *Journal of Hydrology* **376**: 24-33. doi:10.1016/j.jhydrol.2009.07.029

Tufekcioglu A, Raich JW, Isenhart TM, Schultz RC. 2001. Soil respiration within riparian buffers and adjacent crop fields. *Plant and Soil* **229**: 117-124. doi:10.1023/a:1004818422908

Turner CL, Kneisler JR, Knapp AK. 1995. Comparative gas exchange and nitrogen responses of the dominant C_4 grass *Andropogon gerardii* and 5 C_3 forbs to fire and topographic position in tallgrass prairie during wet year. *International Journal of Plant Sciences* **156**: 216-226.

Turner NC. 1991. Measurement and influence of environmental and plant factors on stomatal conductance in the field. *Agricultural and Forest Meteorology* **54**: 137-154. doi:10.1016/0168-1923(91)90003-9

Udawatta RR, Anderson SH, Gantzer CJ, Garrett HE. 2008. Influence of prairie restoration on CT-measured soil pore characteristics. *Journal of Environmental Quality* **37**: 219-228. doi:10.2134/jeq2007.0227

Villarini G, Smith JA, Baeck ML, Vitolo R, Stephenson DB, Krajewski WF. 2011. On the frequency of heavy rainfall for the Midwest of the United States. *Journal of Hydrology* **400**: 103-120. doi:10.1016/j.jhydrol.2011.01.027

Wang S, Fu BJ, Gao GY, Liu Y, Zhou J. 2013. Responses of soil moisture in different land cover types to rainfall events in a re-vegetation catchment area of the Loess Plateau, China. *Catena* **101**: 122-128. doi:10.1016/j.catena2012.10.006

Weaver JE 1954. *North American prairie.* Johnsen Pub. : Lincoln, Neb.

Weibel FP, Devos JA. 1994. Transpiration measurements on apple trees with an improved stem heat balance method *Plant and Soil* **166**: 203-219.

Wever LA, Flanagan LB, Carlson PJ. 2002. Seasonal and interannual variation in evapotranspiration, energy balance and surface conductance in a northern temperate grassland. *Agricultural and Forest Meteorology* **112**: 31-49.

Zhang YK, Schilling KE. 2006. Increasing streamflow and baseflow in Mississippi River since the 1940 s: Effect of land use change. *Journal of Hydrology* **324**: 412-422. doi:10.1016/j.jhydrol.2005.09.033

Table 1 Total growing season *ET*, precipitation and ratio ET/P in 2007 and 2008. Crops were *G. max* in 2007 and *Z. mays* in 2008.

Year	ET (mm)		Precipitation	ET/P	
	Prairie	Crop	(mm)	Prairie	Crop
2007	403.0	379.1	557.1	0.72	0.68
2008	413.4	376.7	776.5	0.53	0.49

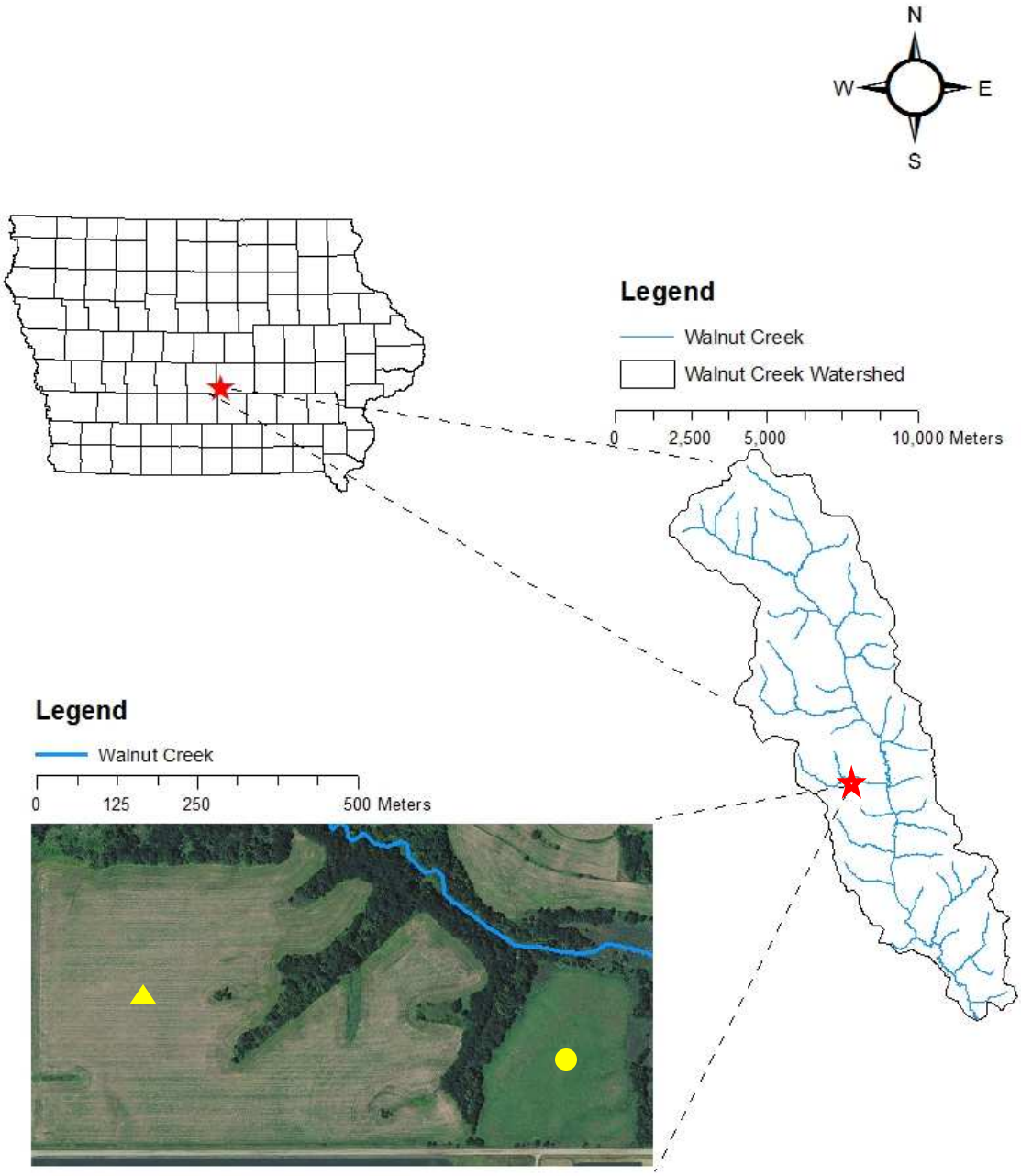


Figure 1. Location of the reconstructed prairie (yellow dot) and the crop field (yellow triangle) within the Walnut Creek watershed in central Iowa.

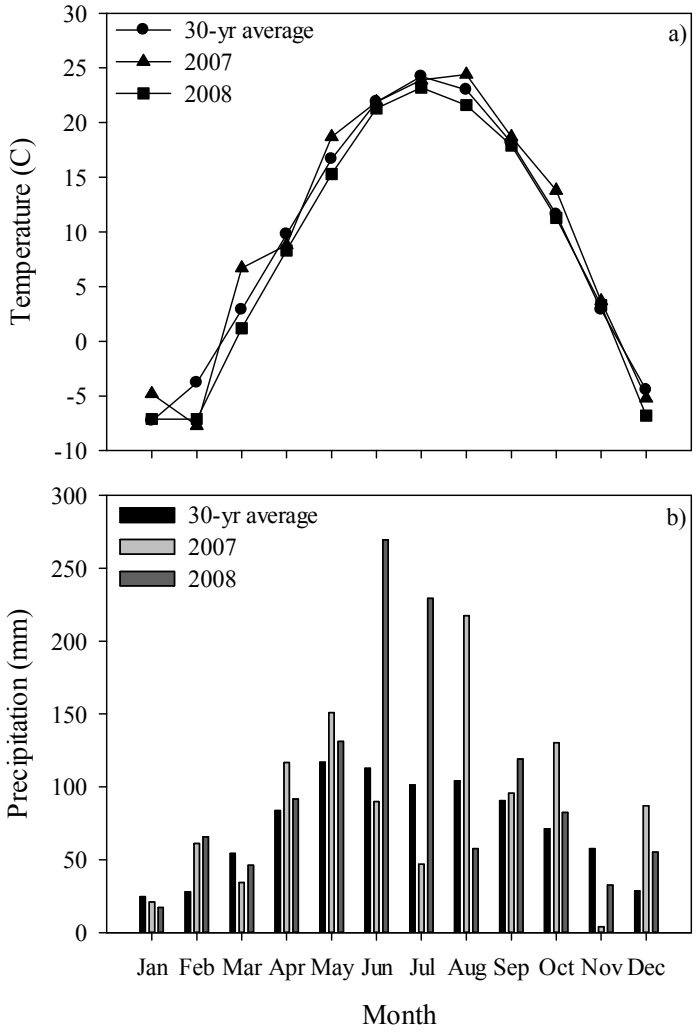


Figure 2. Monthly precipitation (a) and mean temperature (b) for 2007, 2008, and the 30-year average (1979-2008). Data for 2007 and 2008 were obtained from Mesowest (NSW14 station) and the National Oceanic and Atmospheric Administration (Des Moines station). Data for the long-term mean were obtained from the Midwestern Regional Climate Center.

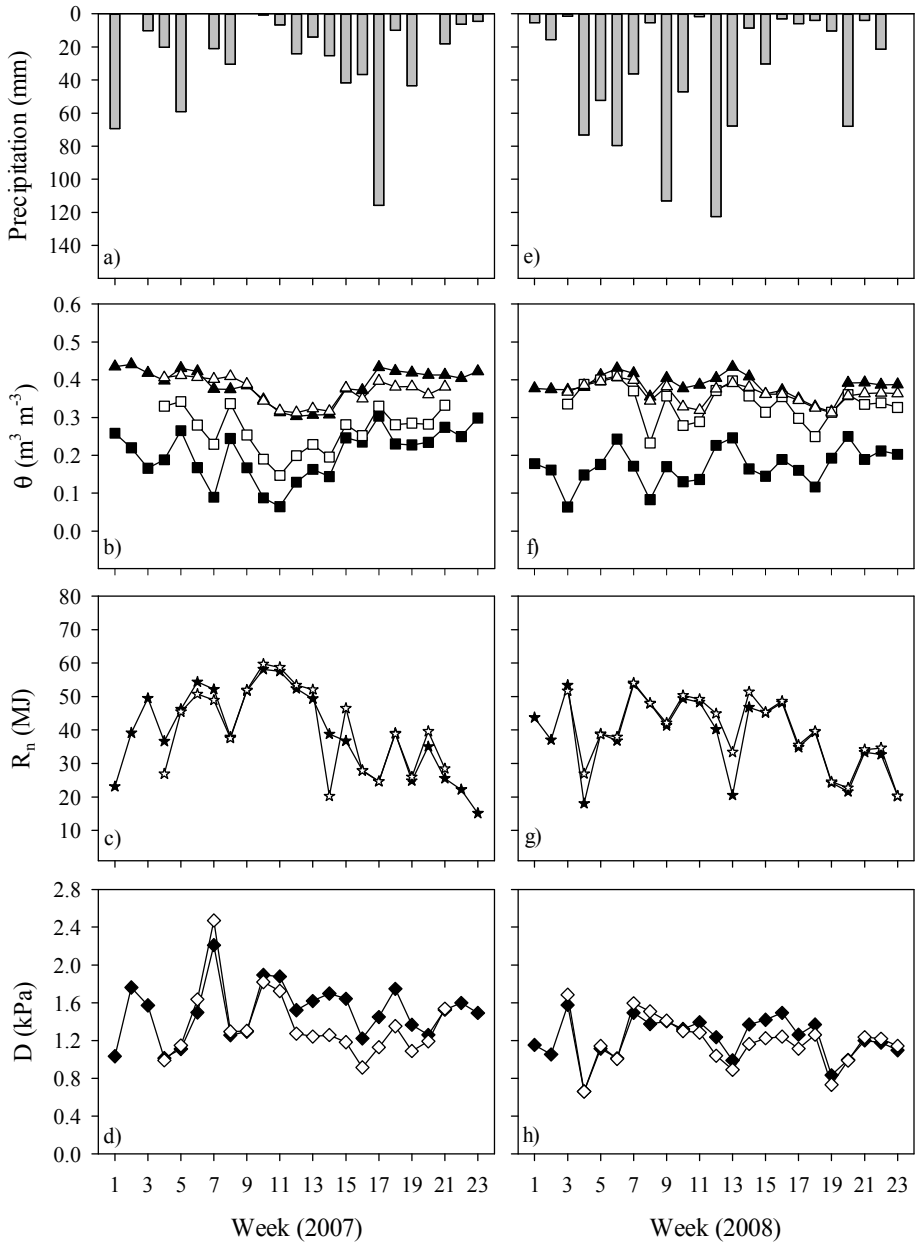


Figure 3. Weekly micrometeorological variables during growing seasons (May 1 - October 5) of 2007 and 2008. Bars in a) and e) represent weekly total precipitation; squares and triangles in b) and f) stand for weekly average soil water content at 0-6 cm ($\theta_{0\text{-}6\ cm}$) and 6-20 cm ($\theta_{6\text{-}20\ cm}$) , respectively; stars in c) and g) symbolize weekly average net radiation (*Rn*); and diamonds in d) and h) show weekly average vapor pressure deficit (*D*). Filled symbols always correspond to prairie, whereas empty symbols represent crop data. Week 23 includes data from only 4 days.

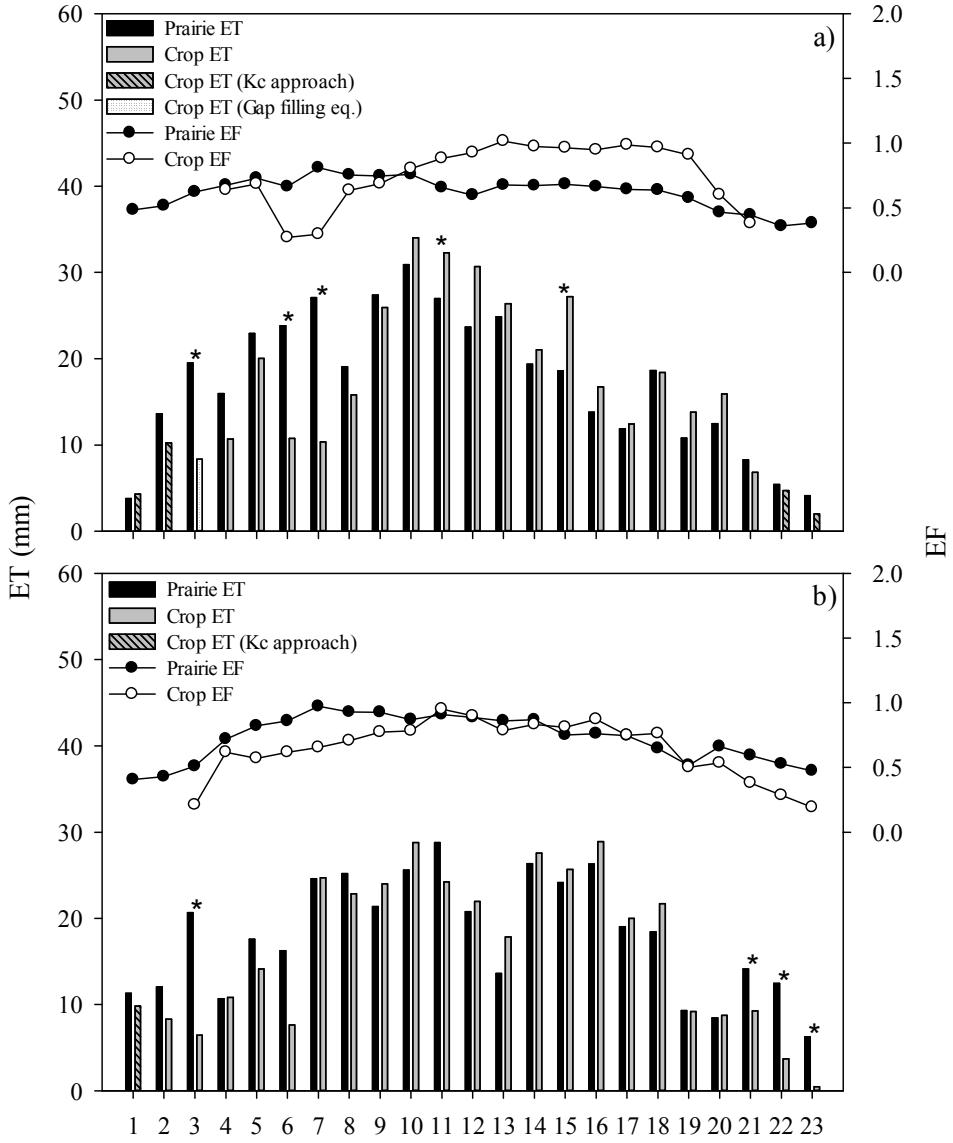


Figure 4. Weekly evapotranspiration (*ET*) and weekly average evaporative fraction (*EF*) during the growing season in 2007 (a) and 2008 (b). Week 23 includes data from only 4 days. Crops were *G. max* in 2007 and *Z. mays* in 2008.Stars show significant difference between sites ($p < 0.05$).

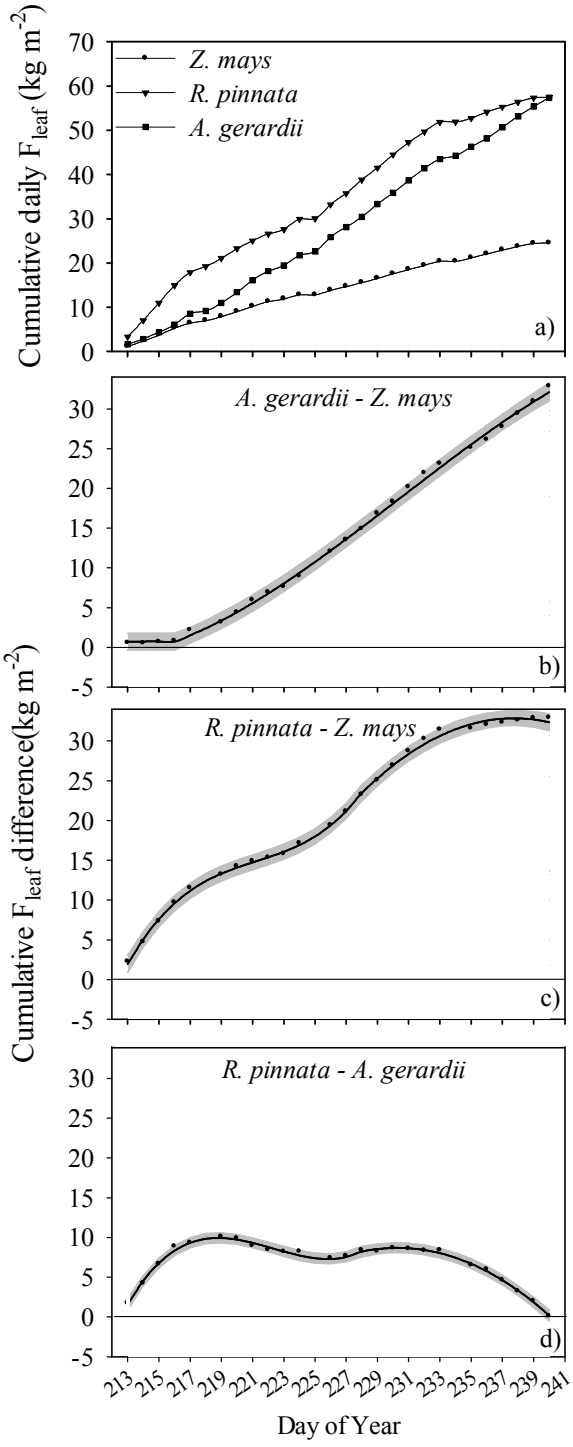


Figure 5. Cumulative daily sap flow (F_{leaf}) for *Z. mays*, *R. pinnata*, *A. gerardii* (a), and cumulative differences between species from Jul 31 to Aug 27: b) *A. gerardii* and *Z. mays*, b) *R. pinnata* and *Z. mays*, and d) *R. pinnata* and *A. gerardii*. Points are observed values, lines are modeled values, and shaded areas encompass the upper and lower confidence intervals (based on a 95% confidence interval). Each point represents an average of 4 to 5 plants.

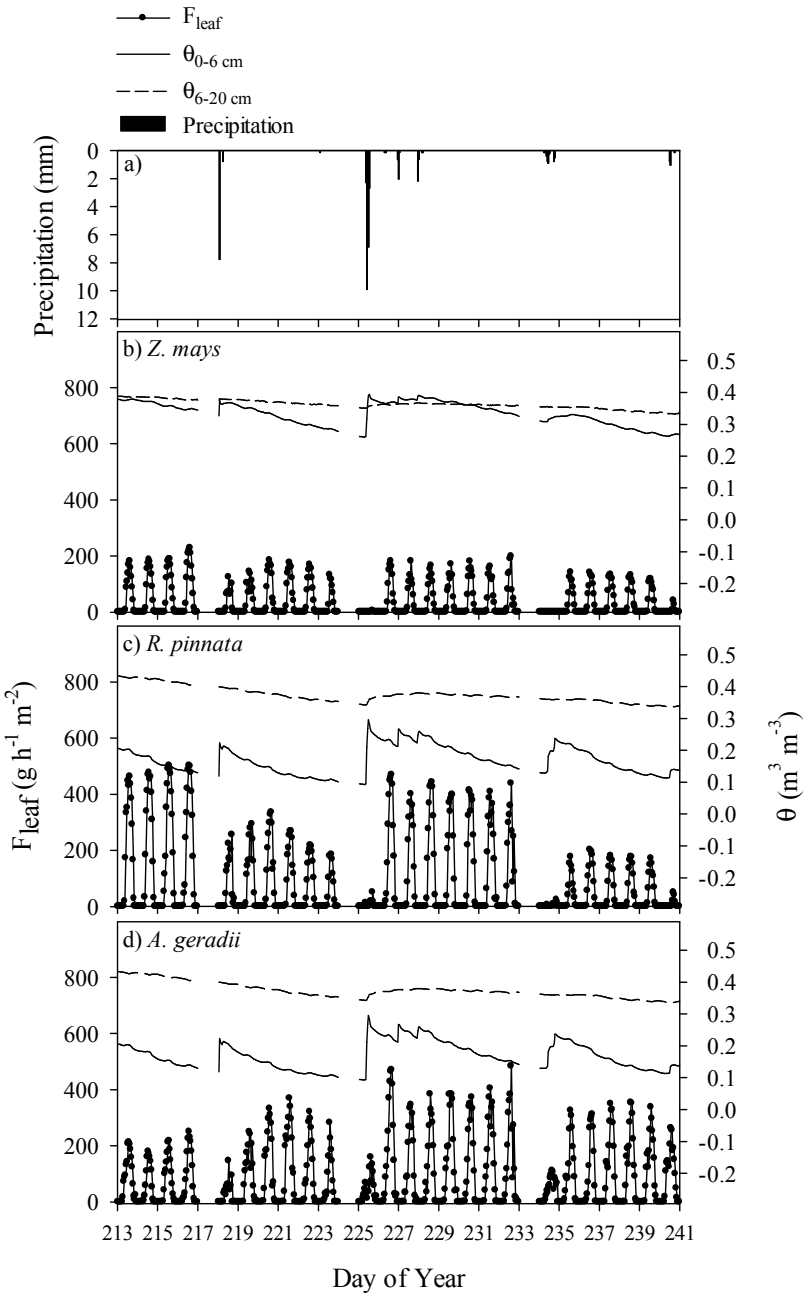


Figure 6. Hourly precipitation (bars), sap flow rates (F_{leaf}, lines with dots), volumetric soil water content from 0 to 6 cm ($\theta_{0\text{-}6\ cm}$, solid lines) and from 6 to 20 cm ($\theta_{6\text{-}20\ cm}$, dashed lines) for a) *Z. mays*, b) *R. pinnata*, and c) *A. gerardii* from Jul 31 to Aug 27. Each point represents an average of 4 to 5 plants.

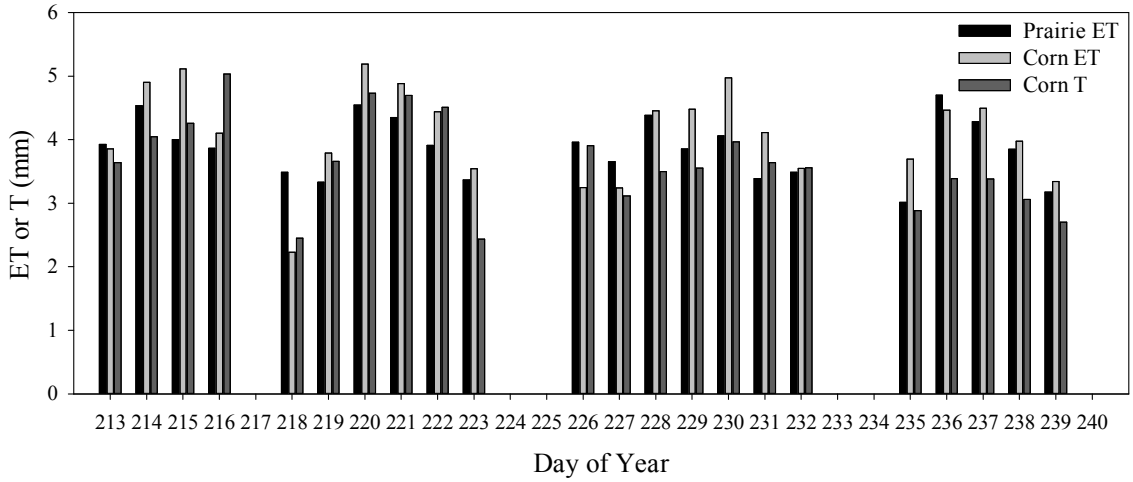


Figure 7. Estimated stand transpiration (*T*) for *Z. mays* and evapotranspiration (*ET*) for both crop and prairie sites during the peak growing season in 2008. Missing days correspond to either rainy days or days when sap flow gauges were rotated.

CHAPTER 3: IDENTIFYING ENVIRONMENTAL DRIVERS OF TRANSPIRATION IN A NATIVE PRAIRIE SPECIES AND TWO CROPS IN A MIXED ANNUAL-PERENNIAL WATERSHED

A paper to be submitted to *Agricultural and Forest Meteorology*

Vilma S. Mateos-Remigio, Thomas J. Sauer, Richard C. Schultz, Heidi Asbjornsen

Abstract

Determining the effect of biophysical parameters on transpiration is important for a better understanding of transpiration patterns in species growing under the same environmental conditions and their potential effect on watershed hydrology. The main objective of this study was to identify what environmental variables are driving hourly transpiration (*Tr*) in native perennial species and crops that are coexisting in a mixed-annual perennial watershed in central Iowa. We collected data for four biophysical variables at two contrasting topographic positions in the watershed during the growing seasons of 2011 and 2012. Whole-plant transpiration was measured in *Zea mays*, *Glycine max* and the most dominant prairie species. *Solidago canadensis* was always dominant at both topographic positions and years; hence, it was used as the representative species for perennial vegetation. For one period in each year, we also analyzed the relationship of plant transpiration with net radiation and vapor pressure deficit. Net radiation was consistently the main driver of transpiration in all species, explaining 70-89% of its hourly variability. During a year with normal precipitation, vapor pressure deficit was the second most important variable

influencing transpiration, but it was displaced by soil water content in a drought year. The effect of wind speed was the least important in both years of study. The relationship of transpiration with net radiation showed a weaker hysteretic effect than that with vapor pressure deficit, which helped to explain why net radiation accounted for higher *Tr* variability. This comparative study at the whole plant level provides insights previously not available about the effect of the most recognized environmental drivers on transpiration of prairie and crop species: net radiation, vapor pressure deficit, soil water content and wind. We conclude that net radiation serves as a valuable approach for estimating *Tr* based on easily obtainable and highly correlated microclimate data.

Introduction

Plant transpiration (*Tr*) is the main mechanism by which water that has fallen to the earth as precipitation is returned to the atmosphere (Schlesinger and Jasechko, 2014) in order to maintain the hydrologic cycle dynamic. This movement of water through plants involves physical and biological processes that interact in a soil-plant-atmosphere continuum. Net radiation (R_n), vapor pressure deficit (D), soil water content (θ) and wind speed (u) are widely considered as the predominant physical or environmental parameters with major control of transpiration (O'Brien et al., 2004; Turner, 1991).

In the Midwestern US, where severe environmental degradation has occurred as a consequence of landscape scale conversion of native prairies to annual row crops, mainly corn (*Zea mays* L.) and soybean (*Glycine max* (L) Merr.), the incorporation of native perennial vegetation in strategic locations within agricultural watersheds is being proposed as an alternative to recuperate hydrologic regulation (Asbjornsen et al., 2014). Because *Tr* is

responsible for the majority of the water exchange, it is crucial to know water use patterns of the adjacent crops and native prairie species in these mixed annual-perennial systems. Given that these patterns are governed to a great extent by multiple environmental variables, a critical first step is determining how species' water use cope with microclimatic variability.

Valuable information about the biophysical controls on annual crops and native perennial species water use is already available from previous research. For example, Li et al. (2005) showed that daily evapotranspiration in a wet temperate grassland was mainly controlled by R_n and D. In another grassland with drier conditions, Li et al. (2007) found that θ was the most important driver of daily water use. They also observed that the evapotranspiration variability explained by D increased as θ became less limited. Likewise, Krishnan et al. (2012) reported a major role of θ on monthly evapotranspiration in a semi-arid grassland. Similarly, studies conducted in soybean and corn fields have shown that light, represented either as R_n or solar radiation (R_s), usually accounts for 73-75 % of the variation in evapotranspiration when there is no water stress (Suyker and Verma, 2009; Ding et al., 2013). As in perennial vegetation, θ has a more important role under dry conditions (Burba and Verma, 2005; Novak et al., 2005).

The consistency of the findings described above suggests that there is a regular pattern in the relationship between plant water use and environmental factors. However, all those studies were conducted at the stand level. While it is reasonable to interpret the response of crop evapotranspiration as a representation of individual plants since they are managed as monoculture, this assumption may not be valid in prairie vegetation, where species with different photosynthetic pathways, morphologies and phenologies coexist. Some studies with tree species (Conard et al., 1997; Du et al., 2011; Oren and Pataki, 2001) have

found that physiological and morphological characteristics (e.g. root length, leaf area and shape) influence the relationships between plant water use and microclimate advocating for a species-specific response to changes in environmental conditions. In contrast, other studies (O'Brien et al., 2004; Kolb and Stone, 2000; Meinzer et al., 2001) have reported this response to be similar among species. Therefore, measurements at the plant level are needed to enhance our understanding about the dynamic relationship between *Tr* and environmental variables. Knowing whether this relationship varies among native perennial plants and annual crops may also help to improve the design of mixed annual-perennial systems in order to maximize the benefits from native perennial vegetation.

Sap flow data collected with thermometric methods are commonly used to estimate whole-plant *Tr* (Smith and Allen, 1996). In trees, measurements can be taken in the same individuals over long time periods allowing determination of water use patterns at long temporal scales (e.g. Ewers et al., 2008; Ghimire et al., 2014; Kumagai et al., 2008; Zhang et al., 2014a). Collecting longer-term data for small herbaceous plants is constrained by several factors including their fast growth rate, vulnerability to physical damage from wind, insects and floods, and their susceptibility to burning due to sensors operation. Consequently, sensors need to be rotated regularly to new plants, and this rotation often produces data gaps. Thus, identifying the most important environmental drivers of *Tr* would also be helpful to predict *Tr* for those periods when data are missed.

The present study was conducted in a mixed annual-perennial watershed during the growing season of two consecutive years with the aim of identifying the environmental variables driving hourly *Tr* in the most dominant prairie species and adjacent crops growing at two contrasting topographic positions. Because R_n and *D* typically exert the greatest

controll on *Tr*, we also assessed the relationship of *Tr* with R_n and *D* during one period of measurements in each year of study.

Materials and Methods

Study area

This research was conducted in a 3-ha experimental watershed located in the Neal Smith National Wildlife Refuge (NSNWR), which is situated within the Walnut Creek watershed in central Iowa (Figure 1). Climate is continental and humid, with an annual precipitation of 874 mm (30-year average, Midwestern Regional Climate Center, MRCC) and the highest monthly rainfall typically occurs in May and June (Schilling and Spooner, 2006).

About 90% of the watershed area is managed under an intensive no-till rotational corn-soybean system. The other 10% is covered by native perennial vegetation distributed in three contour strips (Figure 2): up slope (160 m length and 6.6 m width), sideslope (166 m length and 5.5 m width), and footslope (37 m length and 27 m width). These strips were planted in 2007 with a native forb and grass seed mix from the tall grass prairie in the Refuge. The composition of the seed mix by weight was 27% grasses, 24% forbs, 5% weedy forbs and weedy grasses, and 44% inert matter (Hirsh et al., 2013). By 2011, the forb *Solidago canadensis* L. and two grasses (*Poa compressa* L. and *Poa pratensis* L.) were the most dominant species growing in the strips of 12 experimental watersheds located in the NSNWR (Hirsh et al., 2013), including the one used in this study.

Measurements, that will be described below, were taken during different periods of the growing seasons in 2011 and 2012 in prairie and crop plants (*G. max* in 2011 and *Z. mays*

in 2012) growing in the upslope and footslope of the watershed (Figure 2), in consequence, we always had four study sites within the watershed: prairie upslope, crop upslope, prairie footslope and crop footslope.

Environmental variables

Meteorological stations were installed in the four study sites to measure different environmental parameters (Figure 2). Soil water content [m^{-3} m^{-3}] was measured with reflectometers (CS615, Campbell Scientific Inc., Logan, UT) positioned from 0 to 6 ($\theta_{0\text{-}6\ cm}$) and 6 to 20 cm depths (and $\theta_{6\text{-}20\ cm}$). Vapor pressure deficit [kPa] was calculated as in Campbell and Norman (1998) for within (D_{be}) and above (D_{ab}) the canopy from relative humidity (RH) [%] and air temperature (T_a) [°C] data collected at 0.3 and 2 m above the soil surface (HMP35C, Vaisala, Woburn, MA). Net radiation [W m^{-2}] and wind speed [m s^{-1}] were measured with a net radiometer (Q*7, Radiation and Energy Balance System, Seattle, WA) and a cup anemometer (014A cup anemometer, Met One, Grants Pass, OR), respectively, at 2 m above the soil surface only in crop upslope and prairie footslope. Leaf wetness measurements (LW) [kΩ] were collected with sensors placed at 0.15 m above the ground in the prairie upslope and crop footslope sites (237 L, Campbell Scientific Inc., Logan, UT). All sensor signals were recorded every 10 s and stored as 15-min averages on CR23X dataloggers (Campbell Scientific Inc., Logan, UT). Electrical power was supplied by deep cycle batteries (12 V) recharged by solar panels. Precipitation data were obtained from a station located at approximately 4 km from our study area.

Transpiration measurements

Whole-plant *Tr* was estimated from sap flow measurements [g h^{-1}] using the stem heat balance (SHB) technique. The theory of the method and equations are described extensively in Baker and van Bavel (1987). Sap flow gauges for stem diameters of 3, 5, 7, 19, and 25 mm were constructed in the laboratory following Senock and Ham (1993). Plots of 1 m^2 (1 m x 1m) were demarcated in the four study sites (Figure 2). Two plots were delimited in the perennial strips because vegetation was more heterogeneous and it was important to capture this variability during data collection. On the other hand, given that the strips contain a high diversity of species, we chose only the most dominant ones (usually 1 to 3 species) growing within the plots. Finally, 10 plants per plot were selected for sap flow measurements. When more than one species were found to be dominant in the perennial plots, at least 3 individual per species were sampled.

One gauge was placed on each plant at a minimum height of 10 cm above the ground to minimize errors induced by heat transfer from the soil (Weibel and Devos, 1994), and then gauges were wrapped with 3-cm-thick foam insulation and covered with aluminum foil to reduce errors due to radiation loading. Any leaves located on the stem segment below the gauge were removed and were not included when determining leaf area. Given that these leaves were located in the most shaded portion of the plant canopy, their removal was assumed to result in a negligible underestimation of whole-plant *Tr*. A constant power system was used to supply energy to the gauges between 4:00 h and 21:00 h CST. Each gauge was connected to a cable (9537, Belden Inc., St. Louis, MO) and then to AM16/32 multiplexers and dataloggers (CR-10X and CR1000, Campbell Scientific Inc., Logan, UT). Signals from the gauges were sampled every 60 s and stored as 15-min averages.

Because the continuous energy supply may damage the plants and compromise accuracy of data, gauges have to be rotated to new plants regularly. Hence, gauges were moved to plants in new plots at intervals of 15 to 20 days. At the end of each measurement period, gauges were removed from the plants and they were harvested and brought to the laboratory to measure leaf area (LI-3100, LI-COR Bioscience, Lincoln, NE). Leaf area value from each plant was used to calculate sap flow on a leaf area basis [g h^{-1} m^{-2}].

Data processing and analysis

Although more than one species were measured during some periods in the prairie plots, *S. canadensis* was the dominant species during all periods in both years of study at both topographic positions. For that reason we use *S. canadensis* as our focal species for analysis and comparisons with the crops. In this study we were only interested in daytime transpiration as most water movement through the plants occurs during the day when energy from solar radiation is available. We observed that on some days, plants started to transpire at negative values of R_n; while on other days Tr was still zero when R_n was already positive. We discarded these data by applying a double screening, so that $R_n < 0$ W m^{-2} and $Tr < 5$ g h^{-1} m^{-2} were eliminated. Framing our data within these constraints also removed the effect of dew.

Due to malfunctioning of some sap flow gauges or data loggers, we failed to capture continuous data from 10 plants in each plot every period. Usually, missed data are gap-filled to have a reliable estimation of average sap flow (Kim et al., 2014). However, because a purpose of this study was to develop models to accurately predict Tr from environmental variables, we decided to use only actual data obtained from direct measurements. By excluding data from the gauges that did not operate properly, the number of samples per plot

decreased. To compensate for sample size reduction in the prairie plots, we chose to calculate a single average sap flow from all sensors that worked in the two plots delimited every period.

To make a straightforward characterization of the environmental conditions in the four study sites, we estimated the median value of R_n, D_{ab}, D_{be}, $\theta_{0\text{-}6\ \mathrm{cm}}$, $\theta_{6\text{-}20\ \mathrm{cm}}$, and u over the days used to analyze their relationship with Tr. Median was preferred over mean values because not all the variables exhibited normal distribution and non-parametric tests were used for further analysis. The Mann-Whitney rank sum test was used to find significant differences in R_n by vegetation type and in u by topographic position. Differences in D_{ab}, D_{be}, $\theta_{0\text{-}6\ \mathrm{cm}}$, and $\theta_{6\text{-}20\ \mathrm{cm}}$ among all the study sites were tested with the Kruskal-Wallis one way analysis of variance on ranks, whereas pairwise multiple comparisons were analyzed using Dunn's method. All these analysis were performed with SigmaPlot (Systat Software Inc., San Jose, CA).

Hourly values of the environmental variables were used to analyze their linear effect on hourly Tr. During exploratory analysis, we found that R_n had a clear control on all species' Tr at both topographic positions; therefore, simple linear regression was conducted to assess the R_n-Tr relationship. Coefficient of determination (r^2) from simple linear models was used to determine the amount of variance explained by R_n alone. Due to a high collinearity found between D_{ab} and D_{be}, and because D_{ab} is more commonly measured than D_{be}, the latter was removed from the multivariate analysisO'Brien et al. (2004) used principal component analysis to develop models to predict tree water use from nine environmental variables. In this study, we had fewer variables and there was no need to reduce dimensionality of our data set. Hence, multiple linear models were created by backward

stepwise regression. First we entered all the explanatory variables and then selected only those that had a significant effect at $p < 0.05$. Then, multiple regressions were run again using the significant variables to recalculate r^2. We noticed that even though some variables were statistically significant, removing them from the models did not cause a substantial reduction in r^2. Thus, we removed those variables that did not improve r^2 by more than 3%. The final r^2 was then calculated. Both simple and multiple linear regressions were conducted in R version 3.1.1 (R Project for statistical computing, Vienna, Austria)

Results

Environmental conditions

Long-term average rainfall (1971-2000) is 526 mm from May to September (MRCC). For the same period in 2011 and 2012, a total of 567 and 228 mm of rain were recorded, respectively; which represent a near-normal (2011) and a dry (2012) growing season over the study period. Table 1 shows the median values for the environmental variables across the days selected from each sampling period in 2011 and 2012, and whether there was a significant difference among vegetation type and topographic position. Due to technical problems with the sensors and dataloggers, we were not always able to collect and compare data at both topographic positions. Because both vegetation types are adjacent to each other and the distance between upslope and footslope position is less than 1 km, we anticipated that R_n, D_{ab} and D_{be} would not vary significantly. In 2012, prairie upslope had higher D_{ab} than prairie footslope only during the first period of measurements ($p < 0.05$). As expected, $\theta_{0\text{-}6\ cm}$, $\theta_{6\text{-}20\ cm}$ and u generally exhibited significant differences between topographic positions and

vegetation types during both years ($p < 0.05$). Results for θ agree with findings reported previously for this site (Gutierrez-Lopez *et al*. 2014).

Tr drivers in *S. canadensis*, *G. max* and *Z. mays*

The main objective of this study was to determine which environmental variables had a significant control on hourly *Tr* of the most dominant prairie and crop species growing at our study sites. Backward stepwise regressions allowed us to achieve this objective and also provided us with the best linear models to predict hourly *Tr* based on the input data. Because making comparisons between species was more interesting for the overall purpose of this study, we will emphasize the results from the periods when data were available for both the native perennial species and the crops.

Table 2 shows simple and multiple linear models for *S. canadensis* and *G. max* in 2011. Because D_{ab} in the *G. max* field looked suspiciously low (perhaps due to a faulty sensor), D_{be} was used for the multivariate analysis in this species. For simplicity, we refer to D_{ab} and D_{be} as *D* here after. Models for the same prairie species and *Z. mays* in 2012 are displayed in Table 3. We found that R_n always explained between 70 and 89 % of the total *Tr* variability in all species during both years of study regardless of the contrasting soil water conditions ($p < 0.01$), and the variation explained by R_n was usually higher in the crops than in the perennial species.

Multiple linear regression analysis conducted on 2011 data showed that *D* and *u* also influenced hourly *Tr* (Table 2). Excluding the first period of measurements, $\theta_{0\text{-}6\ cm}$ and $\theta_{6\text{-}20\ cm}$ did not have any effect on hourly *Tr* changes. In contrast, analysis of data collected during 2012 showed that all environmental variables had some control on *Tr* of both species

sampled (Table 3). Nonetheless, as in 2011, effect of environmental variables was not consistent among periods, species and topographic position.

Ranking the environmental variables by number of appearances in the multiple linear models, D and $\theta_{6\text{-}20\ cm}$ were found to be second most important variables in 2011 and 2012, respectively. With a few exceptions, adding at least one more variable usually increased the variability explained by the models. The largest improvements were always for the perennial species, but the highest r^2occurred for the crops. In 2011, r^2 in multiple linear models ranged from 0.83 to 0.97 and from 0.82 to 0.97 in 2012. Figures 3 to 6 show the relationship between measured *Tr* and predicted *Tr* with some of the simple and multiple linear models presented in Table 2 and 3.

Relationship of R_n and *D* with hourly *Tr*

Over short time scales, R_n and D are generally recognized as the most important drivers of *Tr* (Zhang et al., 2014a). In order to determine the response of *Tr* to these two variables separately, their relationship was plotted during one period in 2011 and 2012 when there was data for both species and positions, revealing a clear hysteretic relationship (Figures 7 and 8).

A counterclockwise loop was observed in the relationship of *Tr* with R_n for both species at the upslope position in the near-normal rainfall year (Figures 7a and c), which means *Tr* in the afternoon was greater than in the morning at any given value of R_n. At the footslope, *Tr* was more closely coupled with R_n so that the hysteresis was less evident (Figures 7b and d), and a somewhat hyperbolic curve was exhibited in *S. canadensis* approaching a plateau at approximately 400 W m^{-2}(Figure 7b), which contrasted with the

more linear function displayed by *G. max* (Figure 7d). A different rotation (clockwise) pattern was found in the loops representing the relationship between *Tr* and D_{ab} (Figures 7e-h) meaning that for the same *D* value, morning *Tr* was higher than afternoon *Tr*. Again, a hyperbolic curve was observed in the response of *Tr* to *D* for *S. canadensis* growing in the footslope position, where *Tr* stopped increasing when *D* was higher than 1 kPa.

In 2012, the dry year, an unexpected figure-eight best described the relationship of *Tr* with R_n in both species and topographic positions (Figures 8a-d), as a consequence, two opposite patterns where found through the day. Early morning *Tr* (8:00 to 9:00) was generally lower than evening *Tr* (18:00 to 20:00), which occurred when R_n ranged from 0 to 300 W m^{-2}. On the contrary, *Tr* from 10:00 to 13:00 was higher than *Tr* from 14:00 to 17:00, happening at R_n values larger than 300 W m^{-2}. When exploring differences by species, it was found that *S. canadensis' Tr* was constrained by R_n at 500 W m^{-2} (Figures 8a-b), but no limitation was observed in *Z. mays* (Figures 8c-d). The relationship between *Tr* and *D* was more or less similar to that in the normal year (Figures 8e-h), although *Tr* in the perennial species became stable as *D* reached 2 kPa at both topographic positions (Figures 8e-f), and crop *Tr* did not exhibit any limitation by *D* (Figures 8g-h).

Discussion

Control of R_n on *Tr*

Among all the environmental variables tested in this study, R_n was found to consistently exert the greatest controll on hourly *Tr* in *S. canadensis*, *G. max* and *Z. mays* as it explained more than 70% of *Tr* variability during all the periods sampled in 2011 and 2012. There is a lack of information on whole-plant *Tr* in the literature, but studies conducted

at the leaf and stand level support our result. Ding et al. (2013) found that 73% of half-hourly evapotranspiration in a maize field was explained by R_s in data fitted by a linear relationship. On a daily basis, they found that R_s accounted for 69% of evapotranspiration variability. Also at the stand level, 75% of variability during growing season water use in corn and soybeans was due to R_n in a multiyear study conducted in Nebraska (Suyker and Verma, 2009). A similar percentage (73%) was reported by Irmak and Mutiibwa (2009) for stomatal resistance response to photosynthetic photon flux density in maize leaves in a Nebraska field when the relationship was fitted with a power function. We are not aware of previous studies assessing environmental effects on prairies species *Tr* under field conditions, yet our result seems realistic considering that *S. canadensis* dominated the canopy in the perennial strips and leaves were well exposed.

Although we performed the linear regression analysis without including the hysteresis effect that existed between *Tr* and R_n (Figures 7 and 8), the large variation in *Tr* explained by R_n alone even during the dry year suggests that both variables were tightly coupled. Therefore, R_n could be accurately used as a single factor to predict hourly *Tr*. Nonetheless, including the effect of hysteresis could improve the regression coefficient as was shown by Ma et al. (2008) for a tree species in China.

The fact that R_n usually accounted for a greater proportion of the variation in *Tr* in the crops than in *S. canadesis* (Table 2 and 3) may be explained by the higher uniformity of crop plants and their homogeneous distribution. In contrast, random distribution of perennial species might have created more shading in leaves of some plants than in others, thereby affecting the whole-plant *Tr* response to R_n.

Other environmental drivers of *Tr*

Transpiration at the whole-plant level is driven by the combined impact of several environmental variables (Chang et al., 2014; O'Brien et al., 2004). In this study, D, θ and u interacted irregularly with R_n (the main driver) to control changes in hourly Tr as was shown by multiple linear regression analysis (Table 2 and 3). Most studies relate water use only to radiation and/or evaporative demand (e.g. Du et al., 2011; Li et al., 2005; Ma et al., 2008; Mackay et al., 2007), but under dry conditions soil moisture content becomes important (Burba and Verma, 2005; Chen et al., 2014; Krishnan et al., 2012; Novak et al., 2005). Accordingly, we did not find θ to have an essential role in explaining Tr variations during 2011, the year with no water limitations, whereas its importance as a driver of Tr increased during the 2012 dry year (Table 2).

The ranking of the importance of the environmental variables was influenced by years with the order of $R_n > D > u$ during 2011 when there was no water limitation, and $R_n > \theta_{6\text{-}20\ cm} > D$ in 2012 when soil water was limited. Wind speed in our study was the least important variable, especially in 2012. Other studies that assessed the direct impact of u on water loss from leaves also found it to be weak (Kim et al., 2014; Irmak and Mutiibwa, 2010); however, the indirect impact of u by increasing D was shown to be significant in a study conducted in a temperate forest (Kim et al., 2014). Overall, our results validate that Tr is mostly correlated to R_n and D under normal soil moisture conditions, whereas the significance of D is displaced by θ when the availability of θ is limited.

In 2012, when θ was found to have a significant control on Tr (Table 4), it was observed that the deeper layer ($\theta_{6\text{-}20\ cm}$) was more important than the upper one ($\theta_{0\text{-}6\ cm}$). This may be a result of the extremely low soil water content in the first 6 cm (<0.1 m3 m^{-3}) that

restricted plant water uptake to depths below 6 cm in the soil profile (Asbjornsen et al., 2008; Nippert and Knapp, 2007).

Except for R_n, environmental control on all species' *Tr* was highly inconsistent among periods and topographic position. In this study we did not incorporate the potential effect of plant competition, which may have been important in the prairie plots. For example, in 2012 when $\theta_{6\text{-}20\ cm}$ exhibited an important role in driving *Tr*, a constant impact was expected at the upslope position, since it is known that soil moisture is more limited in uplands (Gutierrez-Lopez et al., 2014; Knapp et al., 1993). However, in period 2 at the upslope position, *Tr* variation in *S. canadensis* was explained only by R_n (Table 3). We attribute this result to lower aboveground biomass productivity occurring at the upslope position (LAI = 1.62 and 1.80 at upslope and footslope, respectively). Lower plant density at the prairie upslope site likely resulted in less light competition and greater exposure of leaves to R_n, such that this single variable could account for most of the *Tr* variability.

Hysteresis on the relationship of *Tr* with R_n and *D*

Hysteresis is created by a phase angle difference between two variables when data are examined over a time series (Zhang et al., 2014b). The hysteretic relationship of *Tr* and R_n and *Tr* and *D* has been addressed in several studies with tree species (O'Brien et al., 2004; Zheng and Wang, 2014; Zheng et al., 2014; Zeppel et al., 2004) since it may impact water use patterns (Zeppel et al., 2004).

We found a constant clockwise response of *Tr* to *D* in the three species assessed, consistent with previous studies (Chen et al., 2014; O'Brien et al., 2004; Zeppel et al., 2004; Zheng and Wang, 2014). In the morning, *Tr* increased with *D*, but in the afternoon, *Tr* was

lower than its morning value at any given *D*. At least three factors have been proposed to explain the rotation of this loop. First, during conditions of high humidity, there is a lag between *D* and R_n that creates hysteresis, and given that *Tr* is more synchronized with R_n, the relationship between *Tr* and *D* also exhibits hysteresis (Zhang et al., 2014b). Second, it has also been suggested that this loop could arise from lower stomatal conductance in the afternoon compared to morning (Zheng et al., 2014). Third, water storage in the stem might also contribute to increased water use rates in the morning (Zeppel et al., 2004). In this study we observed that *D* peaked later than R_n. In addition, hourly stomatal conductance data taken on DOY 222 in 2012 (data not shown) showed that stomatal conductance rates were higher in the morning than in the afternoon for any give value of *D* in both *S. canadensis* and *Z. mays*. Since plants in this study are relatively small compared to trees where water storage might be substantial; we suggest that factors 1 and 2 likely contributed to the hysteresis between *D* and *Tr*.

The response of *Tr* to R_n was varied. In period 2 of 2011, when hysteresis was practically nonexistent at the footslope position in both species (Figures 7b and d), a counterclockwise pattern was detected at the upslope position (Figures 7a and c). According to Zeppel et al. (2004) this rotation may be explained by the lag between R_n and *D*, and the fact that stomatal conductance becomes light-saturated at low levels of radiation, thus, for any value of R_n, *D* is larger in the afternoon than in the morning; as a result, *Tr* will be lower in the morning than in the afternoon when plotted against R_n.

The figure-eight found in 2012 (Figures 8a-d) was also observed in Zheng and Wang (2014) in desert shrub vegetation, but they did not provide any explanation. In this study, we attribute that response to the dry and hot conditions that prevailed during the growing season

making *D* higher than in 2011. From 8:00 to 9:00 in the morning, *Tr* was lower than evening *Tr* (18:00-20:00), as was expected based on Zeppel's (2004) premise. After 9:00 when *D* was already higher than ~0.9 kPa, *Tr* became larger than afternoon *Tr* (14:00 to 17:00) for any given value of R_n higher than 300 W m^{-2}. It is likely that the high evaporative demand present since early morning added to the high available energy prompted a rise in *Tr* rates and created the clockwise rotation as in the *D*-*Tr* relationship. We looked at data from other periods and observed the same response for days when *D* reached values close to 1 kPa by 9:00 in the morning and a maximum daily *D* higher than 2.5 kPa.

Interestingly in 2012, *S. canadensis' Tr* was restricted at high rates of R_n and *D* (R_n > 500 W m^{-2} and *D* > 2 kPa) at both topographic positions, but not *Z. mays'* which exhibited an almost linear response to both variables. Gholipoor et al. (2013) assessed the *Tr* response to *D* in 35 hybrids of *Z. mays* and found that only 11 were sensitive to increasing *D*. We plotted *Tr* against R_n and *D* for all periods of measurement in both species (plots no shown) and found that *Tr* was consistently restricted in *S. canadensis*. These results suggest a greater degree of stomatal sensitivity to moisture stress and, hence, more conservative water use by the native prairie species compared to the annual crops.

Hysteresis was found in the response of *Tr* to R_n in both years of study, but the area was smaller than in the loop between *Tr* and *D*. It demonstrates that *Tr* is more in phase with R_n, and therefore, this environmental variable is able to account for a greater proportion of hourly *Tr* variation.

Limitations to the study

The SHB method has been proven to provide accurate continuous measurements of sap flow that can be used as a direct estimate of *Tr* in small plants. Nonetheless, because of the size of the plants, the heat applied to operate the gauges may damage the stem, and it represented the main limitation in this study, as data from each period of measurements were collected in new plants growing in different plots. For every period, we assumed there were no physiological differences among individual plants that could affect the response to environmental parameters. However, we are aware of potential variability added by the size of the plants and their spatial distribution within plots which may have influenced the response (to R_n and u, mainly) among periods. For example, in period 1 and 2 of 2012, R_n explained 89% of *Tr* variation in *S. canadensis* at the upslope position, but this percentage decreased to 79% in period 3. It may be possible that plants measured in period 3 were more shaded than those in period 1 and 2. Therefore, we analyzed data for each period separately, although it restricted us from making seasonal assessments.

Given that the watershed is managed under a crop rotation system, we were not able to make comparisons among years for each crop, which would have been interesting since during the study years water availability and evaporative demand varied significantly.

Conclusions

In this study we assessed the response of hourly *Tr* in one native prairie species and two crops to four environmental variables known to play an important role in driving the diurnal course of *Tr*: R_n, D, θ (at two depths) and u. Based on the determination coefficients from simple linear models that ranged from 70 to 89%, we found that R_n was always the

main driver of *Tr* in all three species at both topographic positions. The influence of the other variables, determined by their recurrence in the multiple linear models, was not consistent within and among periods of measurements, but when comparing general patterns among years, we observed that *D* was the second most important variable during the year with normal conditions of soil water availability. In the dry year, θ played a more significant role than *D*. The direct effect of *u* on *Tr* was typically less important in both years of study.

One period of measurement from each year was used to display the diurnal relationship of *Tr* with R_n and *D*, and a hysteretic relationship was found. Whereas the response of *T*r to *D* always exhibited at clockwise rotation in both years and in the three species measured, the response to R_n showed more variations. Still, the hysteretic area was smaller in *Tr*-R_n than *Tr*-*D*, supporting the contention that R_n can be used as a single factor to predict *Tr* when data from other variables are not available.

Despite the limitations of this research, to our knowledge, this is the first study simultaneously assessing the control of environmental variables on *Tr* of a native prairie species and crops growing adjacently at contrasting topographic positions. Thus, our results provide information that is fundamental to improve our understanding concerning the potential benefits of restoring perennial vegetation within watersheds typically dominated by annual row crops.

Acknowledgements

This research was supported by the Iowa State University's College of Agriculture and Life Sciences; the Leopold Center for Sustainable Agriculture; the U.S. Department of Agriculture's National Research Initiative, Agriculture and Food Research Initiative, and

Sustainable Agriculture Research and Education programs; and the U.S. Forest Service. We thank Forrest Goodman, Chris Witte, Gabriela Lopez-Flores and Omar de Kok-Mercado for their help in deploying the equipment used during this research and collecting the data.

References

Asbjornsen, H., Hernandez-Santana, V., Liebman, M., Bayala, J., Chen, J., Helmers, M., Ong, C.K.,Schulte, L.A., 2014. Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. Renewable Agric. Food Syst. 29(2), 101-125.

Asbjornsen, H., Shepherd, G., Helmers, M.,Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern US. Plant and Soil. 308(1-2), 69-92.

Baker, J.M.,van Bavel, C.H.M., 1987. Measurement of mass flow of water in the stems of herbaceous plants. Plant Cell Environ. 10(9), 777-782.

Burba, G.G.,Verma, S.B., 2005. Seasonal and interannual variability in evapotranspiration of native tallgrass prairie and cultivated wheat ecosystems. Agric. For. Meteorol. 135(1-4), 190-201.

Campbell, G.S.,Norman, J.M., 1998. An Introduction to Environmental Biophysics. Springer, New York.

Chang, X.X., Zhao, W.Z.,He, Z.B., 2014. Radial pattern of sap flow and response to microclimate and soil moisture in Qinghai spruce (*Picea crassifolia*) in the upper Heihe River Basin of arid northwestern China. Agric. For. Meteorol. 187, 14-21.

Chen, D.Y., Wang, Y.K., Liu, S.Y., Wei, X.G.,Wang, X., 2014. Response of relative sap flow to meteorological factors under different soil moisture conditions in rainfed jujube (*Ziziphus jujuba* Mill.) plantations in semiarid Northwest China. Agric. Water Manage. 136, 23-33.

Conard, S.G., Sparks, S.R.,Regelbrugge, J.C., 1997. Comparative plant water relations and soil water depletion patterns of three seral shrub species on forest sites in southwestern Oregon. For. Sci. 43(3), 336-347.

Ding, R.S., Kang, S.Z., Li, F.S., Zhang, Y.Q.,Tong, L., 2013. Evapotranspiration measurement and estimation using modified Priestley-Taylor model in an irrigated maize field with mulching. Agric. For. Meteorol. 168, 140-148.

Du, S., Wang, Y.L., Kume, T., Zhang, J.G., Otsuki, K., Yamanaka, N.,Liu, G.B., 2011. Sapflow characteristics and climatic responses in three forest species in the semiarid Loess Plateau region of China. Agric. For. Meteorol. 151(1), 1-10.

Ewers, B.E., Mackay, D.S., Tang, J., Bolstad, P.V.,Samanta, S., 2008. Intercomparison of sugar maple (*Acer saccharum* Marsh.) stand transpiration responses to environmental conditions from the Western Great Lakes Region of the United States. Agric. For. Meteorol. 148(2), 231-246.

Ghimire, C.P., Lubczynski, M.W., Bruijnzeel, L.A.,Chavarro-Rincón, D., 2014. Transpiration and canopy conductance of two contrasting forest types in the Lesser Himalaya of central Nepal. Agric. For. Meteorol. 197, 76-90.

Gholipoor, M., Choudhary, S., Sinclair, T.R., Messina, C.D.,Cooper, M., 2013. Transpiration response of maize hybrids to atmospheric vapour pressure deficit. J. Agron. Crop Sci. 199(3), 155-160.

Gutierrez-Lopez, J., Asbjornsen, H., Helmers, M.,Isenhart, T., 2014. Regulation of soil moisture dynamics in agricultural fields using strips of native prairie vegetation. Geoderma. 226, 238-249.

Hirsh, S.M., Mabry, C.M., Schulte, L.A.,Liebman, M., 2013. Diversifying agricultural catchments by incorporating tallgrass prairie buffer strips. Ecol. Restor. 31(2), 201-211.

Irmak, S.,Mutiibwa, D., 2009. On the dynamics of stomatal resistances: relationships between stomatal behavior and micrometeorological variables and performance of Jarvis-Type parameterization. Trans. ASABE. 52(6), 1923-1939.

Irmak, S.,Mutiibwa, D., 2010. On the dynamics of canopy resistance: Generalized linear estimation and relationships with primary micrometeorological variables. Water Resour. Res. 46, W08526.

Kim, D., Oren, R., Oishi, A.C., Hsieh, C.I., Phillips, N., Novick, K.A.,Stoy, P.C., 2014. Sensitivity of stand transpiration to wind velocity in a mixed broadleaved deciduous forest. Agric. For. Meteorol. 187, 62-71.

Knapp, A.K., Fahnestock, J.T., Hamburg, S.P., Statland, L.B., Seastedt, T.R.,Schimel, D.S., 1993. Landscape patterns in soil plant water relations and primary productivity in tallgrass prairie. Ecology. 74(2), 549-560.

Kolb, T.E.,Stone, J.E., 2000. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine-oak forest. Tree Physiol. 20(1), 1-12.

Krishnan, P., Meyers, T.P., Scott, R.L., Kennedy, L.,Heuer, M., 2012. Energy exchange and evapotranspiration over two temperate semi-arid grasslands in North America. Agric. For. Meteorol. 153, 31-44.

Kumagai, T., Tateishi, M., Shimizu, T.,Otsuki, K., 2008. Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed. Agric. For. Meteorol. 148(10), 1444-1455.

Li, S.G., Asanuma, J., Kotani, A., Davaa, G.,Oyunbaatar, D., 2007. Evapotranspiration from a Mongolian steppe under grazing and its environmental constraints. J. Hydrol. 333(1), 133-143.

Li, S.G., Lai, C.T., Lee, G., Shimoda, S., Yokoyama, T., Higuchi, A.,Oikawa, T., 2005. Evapotranspiration from a wet temperate grassland and its sensitivity to microenvironmental variables. Hydrol. Process. 19(2), 517-532.

Ma, L., Lu, P., Zhao, P., Rao, X.Q., Cai, X.A.,Zeng, X.P., 2008. Diurnal, daily, seasonal and annual patterns of sap-flux-scaled transpiration from an Acacia mangium plantation in South China. Ann. For. Sci. 65(4).

Mackay, D.S., Ewers, B.E., Cook, B.D.,Davis, K.J., 2007. Environmental drivers of evapotranspiration in a shrub wetland and an upland forest in northern Wisconsin. Water Resour. Res. 43(3).

Meinzer, F.C., Goldstein, G.,Andrade, J.L., 2001. Regulation of water flux through tropical forest canopy trees: Do universal rules apply? Tree Physiol. 21(1), 19-26.

Nippert, J.B.,Knapp, A.K., 2007. Linking water uptake with rooting patterns in grassland species. Oecologia. 153(2), 261-272.

Novak, V., Hurtalova, T.,Matejka, F., 2005. Predicting the effects of soil water content and soil water potential on transpiration of maize. Agric. Water Manage. 76(3), 211-223.

O'Brien, J.J., Oberbauer, S.F.,Clark, D.B., 2004. Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. Plant Cell Environ. 27(5), 551-567.

Oren, R.,Pataki, D.E., 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia. 127(4), 549-559.

Schilling, K.E.,Spooner, J., 2006. Effects of watershed-scale land use change on stream nitrate concentrations. J. Environ. Qual. 35(6), 2132-2145.

Schlesinger, W.H.,Jasechko, S., 2014. Transpiration in the global water cycle. Agric. For. Meteorol. 189, 115-117.

Senock, R.S.,Ham, J.M., 1993. Heat balance sap flow gauge for small diameter stems. Plant Cell Environ. 16(5), 593-601.

Smith, D.M.,Allen, S.J., 1996. Measurement of sap flow in plant stems. J. Exp. Bot. 47(305), 1833-1844.

Suyker, A.E.,Verma, S.B., 2009. Evapotranspiration of irrigated and rainfed maize-soybean cropping systems. Agric. For. Meteorol. 149(3-4), 443-452.

Turner, N.C., 1991. Measurement and influence of environmental and plant factors on stomatal conductance in the field. Agric. For. Meteorol. 54(2-4), 137-154.

Weibel, F.P.,Devos, J.A., 1994. Transpiration measurements on apple trees with an improved stem heat balance method. Plant and Soil. 166(2), 203-219.

Zeppel, M.J.B., Murray, B.R., Barton, C.,Eamus, D., 2004. Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. Funct. Plant Biol. 31(5), 461-470.

Zhang, J.-G., Guan, J.-H., Shi, W.-Y., Yamanaka, N.,Du, S., 2014a. Interannual variation in stand transpiration estimated by sap flow measurement in a semi-arid black locust plantation, Loess Plateau, China. Ecohydrology. DOI:10.1002/eco.1495.

Zhang, Q., Manzoni, S., Katul, G., Porporato, A.,Yang, D., 2014b. The hysteretic evapotranspiration- Vapor pressure deficit relation. J. Geophys. Res. G:Biogeosci. 119(2), 125-140.

Zheng, C.,Wang, Q., 2014. Water-use response to climate factors at whole tree and branch scale for a dominant desert species in central Asia: *Haloxylon ammodendron*. Ecohydrology. 7(1), 56-63.

Zheng, H., Wang, Q., Zhu, X., Li, Y.,Yu, G., 2014. Hysteresis responses of evapotranspiration to meteorological factors at a diel timescale: patterns and causes. Plos One. 9(6).

Table 1. Median values for net radiation (R_n), vapor pressure deficit below and above the canopy (D_{be} and D_{ab}, respectively), volumetric soil water content at 0-6 cm ($\theta_{0\text{-}6\ cm}$) and 6-20 cm ($\theta_{6\text{-}20\ cm}$) depth, and wind speed (u), during the days used to assess their relationship with hourly transpiration (Tr) in a mixed annual-perennial watershed in central Iowa during the growing seasons of 2011 and 2012. Superscript letters indicate significant difference ($p < 0.05$).

2011								
Period/ Day of year	Vegetation	Topographic Position	Micrometeorological variables					
			R_n * (W m^{-2})	D_{be} (kPa)	D_{ab} (kPa)	$\theta_{0\text{-}6\ cm}$ (m^3 m^{-3})	$\theta_{6\text{-}20\ cm}$ (m^3 m^{-3})	u ** (m s^{-1})
1 189,195-196,198-199	Prairie	Upslope	319.800	0.726			0.242	3.271
2 211-215	Prairie	Upslope	322.175	1.007	1.050	0.129^a	0.273^a	2.011^a
		Footslope		1.033	0.887	0.269^b	0.237^b	1.470^b
	Crop	Upslope	320.212	1.093		0.125^c	0.291^c	
		Footslope		1.231		0.135^a	0.268^a	
3 232-236	Prairie	Upslope	288.775	0.908	1.068	0.113^a	0.233^a	2.107^a
		Footslope		0.950	1.040	0.157^b	0.281^b	1.548^b
	Crop	Upslope	276.800	0.998		0.083^c	0.265^c	
		Footslope		1.039		0.098^d	0.218^d	
2012								
Period/ Day of year	Vegetation	Topographic Position	Micrometeorological variables					
			R_n * (W m^{-2})	D_{be} (kPa)	D_{ab} (kPa)	$\theta_{0\text{-}6\ cm}$ (m^3 m^{-3})	$\theta_{6\text{-}20\ cm}$ (m^3 m^{-3})	u ** (m s^{-1})
1 160-162, 164-166	Prairie	Upslope	345.563	1.540	1.843^a	0.079^a	0.184^a	4.845^a
		Footslope		1.612	1.433^b	0.076^b	0.159^b	3.572^b
2 188-189, 192-194	Prairie	Upslope	292.650	1.204	1.644	0.079^a	0.176^a	2.392^a
		Footslope		1.449	1.458	0.123^b	0.164^b	2.075^b
	Crop	Upslope	346.450	1.632	1.418	0.030^c	0.255^c	
3 213-216, 219-220	Prairie	Upslope	320.050	1.542	2.443	0.067^a	0.172^a	1.945^a
		Footslope		1.813	1.948	0.088^b	0.157^b	1.774^b
	Crop	Upslope	338.075	2.059	2.522	0.034^c	0.236^c	
		Footslope		1.978	2.174	0.030^d	0.207^d	
4 252-256	Prairie	Upslope	305.212	1.399	1.902	0.0623^a	0.161^a	3.898^a
		Footslope		1.424	1.718	0.0807^b	0.146^b	3.036^b

* R_n was tested by vegetation type.

** u was tested by topographic position.

Table 2. Parameters, estimates and statistics of simple and multiple linear models for *S. canadensis* and *G. max* at two contrasting topographic positions in a mixed annual-perennial watershed and at different periods during the growing season of 2011.

Period	Species	Topographic position	Simple linear model				r^2	Multiple linear model				r^2
			Parameter	Estimate	SE	p		Parameter	Estimate	SE	p	
1	*S. canadensis*	Upslope	Intercept	23.614	17.333		0.743	Intercept	404.600	63.600		0.843
			R_n	0.574	0.044	0.000		R_n	0.555	0.034	0.000	
								$\theta_{6\text{-}20\ cm}$	-1539.000	250.900	0.000	
2	*S. canadensis*	Upslope	Intercept	56.524	19.438		0.786	Intercept	-104.483	21.455		0.930
			R_n	0.708	0.048	0.000		R_n	0.412	0.039	0.000	
								D	163.755	16.333	0.000	
								u	33.993	7.667	0.000	
		Footslope	Intercept	55.392	13.189		0.792	Intercept	-3.134	20.261		0.829
			R_n	0.513	0.034	0.000		R_n	0.472	0.033	0.000	
								u	46.649	12.975	0.000	
		Upslope	Intercept	-0.736	7.739		0.839	Intercept	-58.931	7.193		0.968
	G. max		R_n	0.347	0.020	0.000		R_n	0.298	0.012	0.000	
								D	63.738	10.334	0.000	
		Footslope	Intercept	-18.235	9.341		0.894	Intercept	-102.173	9.569		0.967
			R_n	0.531	0.024	0.000		R_n	0.469	0.015	0.000	
								D	27.046	3.947	0.000	
								u	43.051	5.163	0.000	
3	*S. canadensis*	Upslope	Intercept	6.267	11.803		0.741	Intercept	-31.263	6.935		0.931
			R_n	0.384	0.032	0.000		R_n	0.257	0.019	0.000	
								D	68.092	5.762	0.000	
	G. max	Upslope	Intercept	-1.445	12.358		0.859	Intercept	-60.033	7.521		0.967
			R_n	0.627	0.035	0.000		R_n	0.527	0.019	0.000	
								D	80.340	6.156	0.000	
			Intercept	-15.452	12.494		0.811	Intercept	-63.601	6.150		0.967
			R_n	0.511	0.035	0.000		R_n	0.425	0.016	0.000	
								D	60.897	3.974	0.000	

Table 3. Parameters, estimates and statistics of simple and multiple linear models for *S. canadensis* and *Z. mays* at two contrasting topographic positions in a mixed annual-perennial watershed and at different periods during the growing season of 2012.

Period	Species	Topographic position	Simple linear model					Multiple linear model				
			Parameter	Estimate	SE	*p*	r^2	Parameter	Estimate	SE	*p*	r^2
1	*S. canadensis*	Upslope	Intercept	14.345	10.475		0.891	Intercept	-615.054	79.877		0.939
			R_n	0.700	0.027	0.000		R_n	0.669	0.021	0.000	
								$\theta_{0\text{-}6\ cm}$	8113.020	1024.585	0.000	
		Footslope	Intercept	22.703	8.243		0.790	Intercept	-1729.000	210.600	0.000	0.929
			R_n	0.337	0.020	0.000		R_n	0.311	0.013	0.000	
								$\theta_{6\text{-}20\ cm}$		1328.000	0.000	
								u	10720.000	2.139	0.000	
									16.080			
2	*S. canadensis*	Upslope	Intercept	34.119	8.111		0.889					
			R_n	0.501	0.022	0.000						
		Footslope	Intercept	7.317	7.175		0.795	Intercept	-218.599	37.642		0.876
			R_n	0.279	0.019	0.000		R_n	0.267	0.015	0.000	
								$\theta_{6\text{-}20\ cm}$	1358.864	223.874	0.000	
	Z. mays	Upslope	Intercept	13.948	6.395		0.885	Intercept	-669.355	86.085		
			R_n	0.315	0.015	0.000		R_n	0.229	0.011	0.000	0.973
								D	35.353	3.034	0.000	
								$\theta_{6\text{-}20\ cm}$	2572.081	333.424	0.000	
3	*S. canadensis*	Upslope	Intercept	5.631	6.175		0.742	Intercept	-711.231	137.914		0.821
			R_n	0.212	0.016	0.000		R_n	0.226	0.014	0.000	
								$\theta_{6\text{-}20\ cm}$	4164.188	800.562	0.000	
		Footslope	Intercept	25.930	6.551		0.847					
			R_n	0.317	0.016	0.000						
	Z. mays	Upslope	Intercept	-9.296	8.578		0.846					
			R_n	0.407	0.021	0.000						

Table 3. Continued.

Period	Species	Topographic position	Simple linear model					Multiple linear model				
			Parameter	Estimate	SE	*p*	r^2	Parameter	Estimate	SE	*p*	r^2
3	*Z. mays*	Footslope	Intercept	15.416	8.232		0.873					
			R_n	0.399	0.020	0.000						
4	*S. canadensis*	Upslope	Intercept	25.797	6.907		0.832	Intercept	9.117	6.187		0.897
			R_n	0.320	0.020	0.000		R_n	0.270	0.018	0.000	
								D	16.580	2.879	0.000	
		Footslope	Intercept	42.995	13.173		0.700	Intercept	6.918	9.258		0.884
			R_n	0.383	0.036	0.000		R_n	0.217	0.029	0.000	
								D	50.684	5.814	0.000	

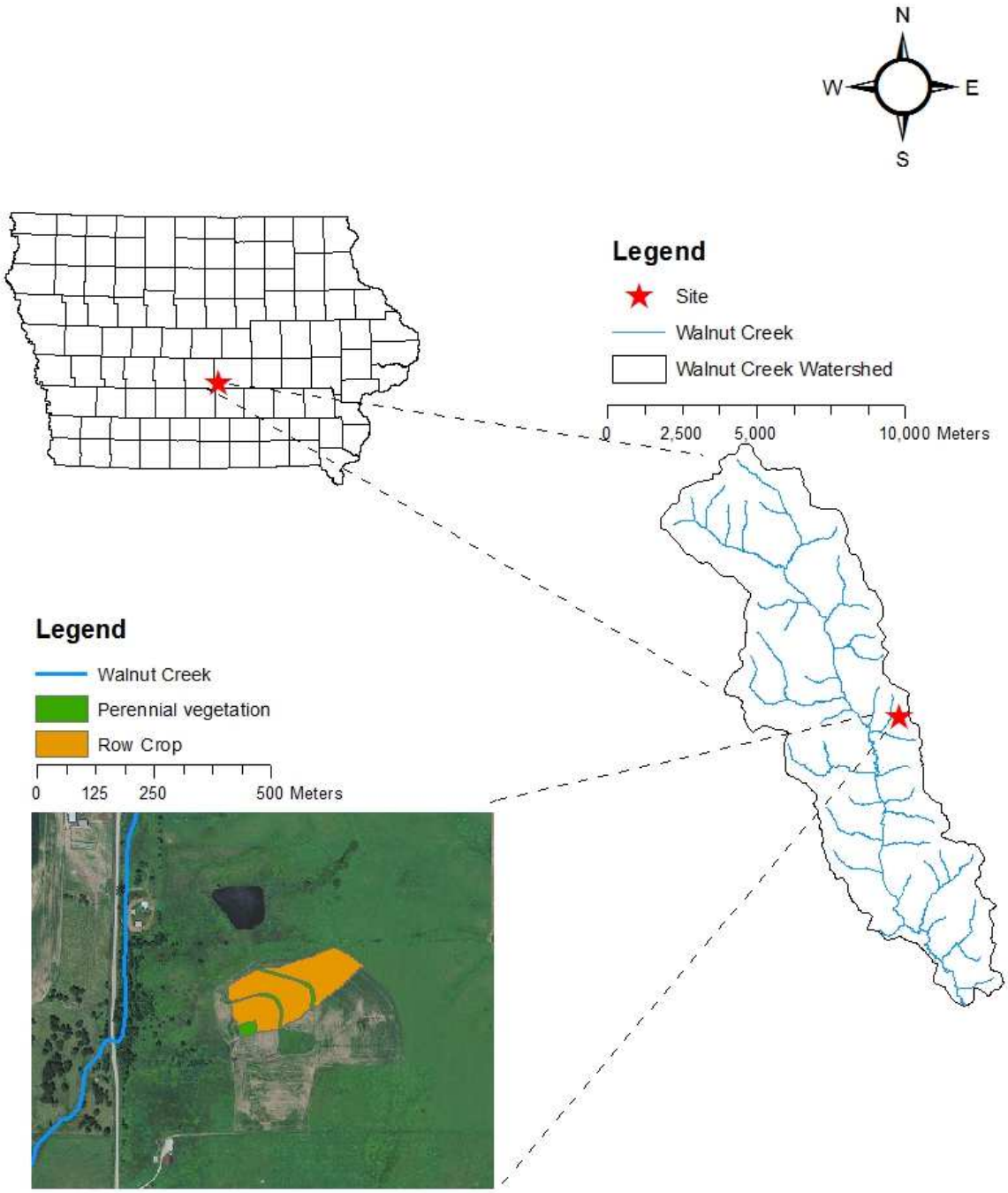


Figure 1. Location of the mixed annual-perennial watershed within the Walnut Creek watershed in central Iowa.

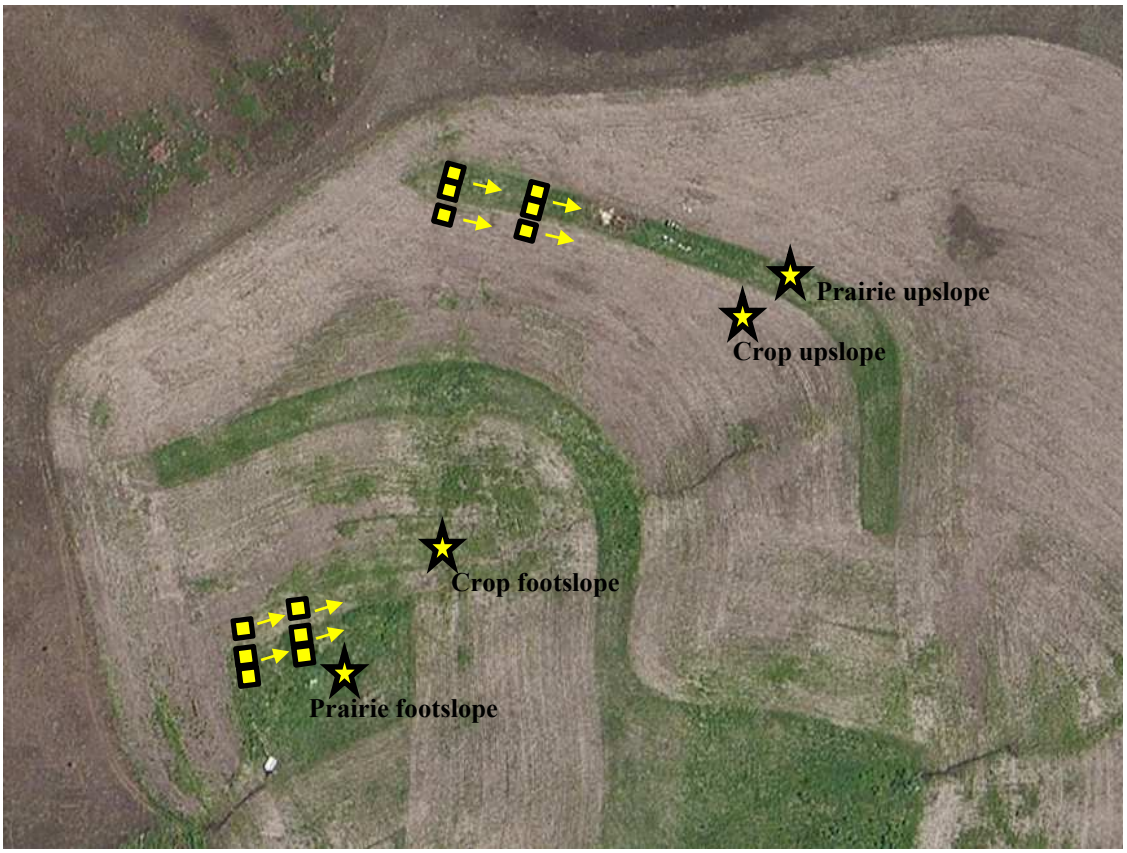


Figure 2. Study sites in a mixed annual-perennial watershed in central Iowa. Stars show approximate location of micrometeorological stations. Squares and arrows represent sap flow plots and direction of plots rotation.

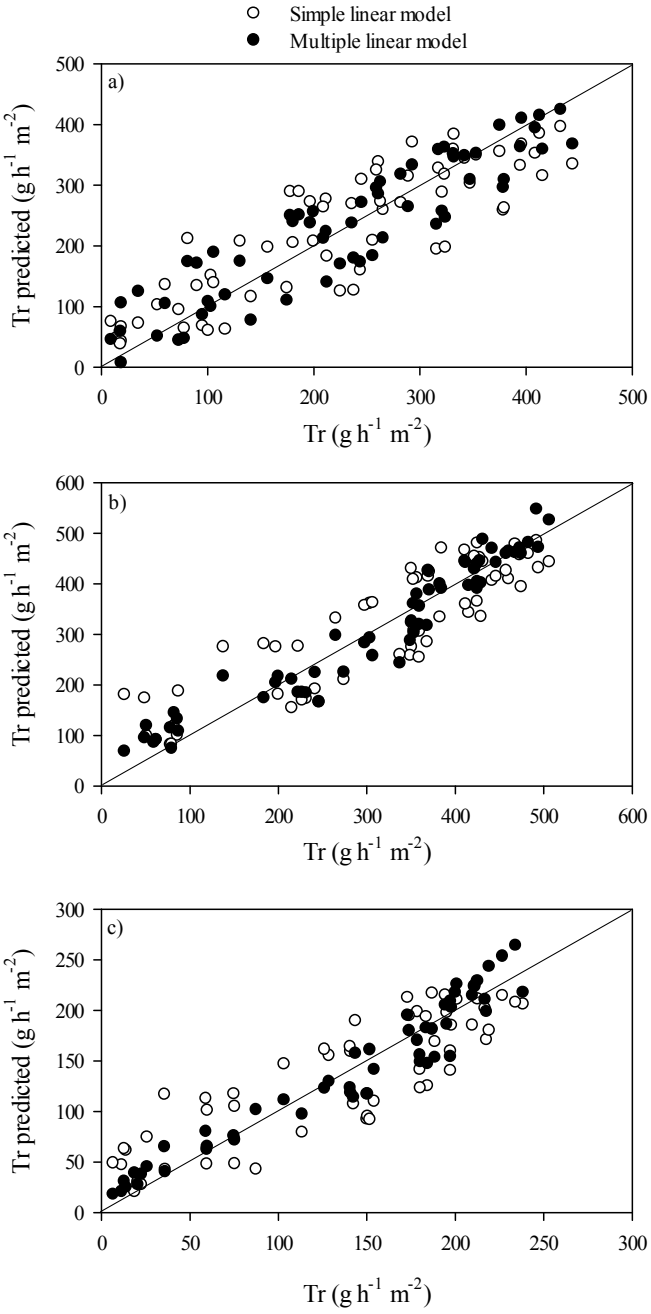


Figure 3. Relationship between transpiration measured (*Tr*) and predicted (*Tr* predicted) in *S. canadensis* growing at the upslope position in period 1 (a, DOY 189, 195-196 and 199), 2 (b, DOY 211-215) and 3 (c, DOY 232-236) during 2011. See Table 2 for parameters, estimates and coefficients of determination. Straight line represents a 1:1 relationship and was included for reference.

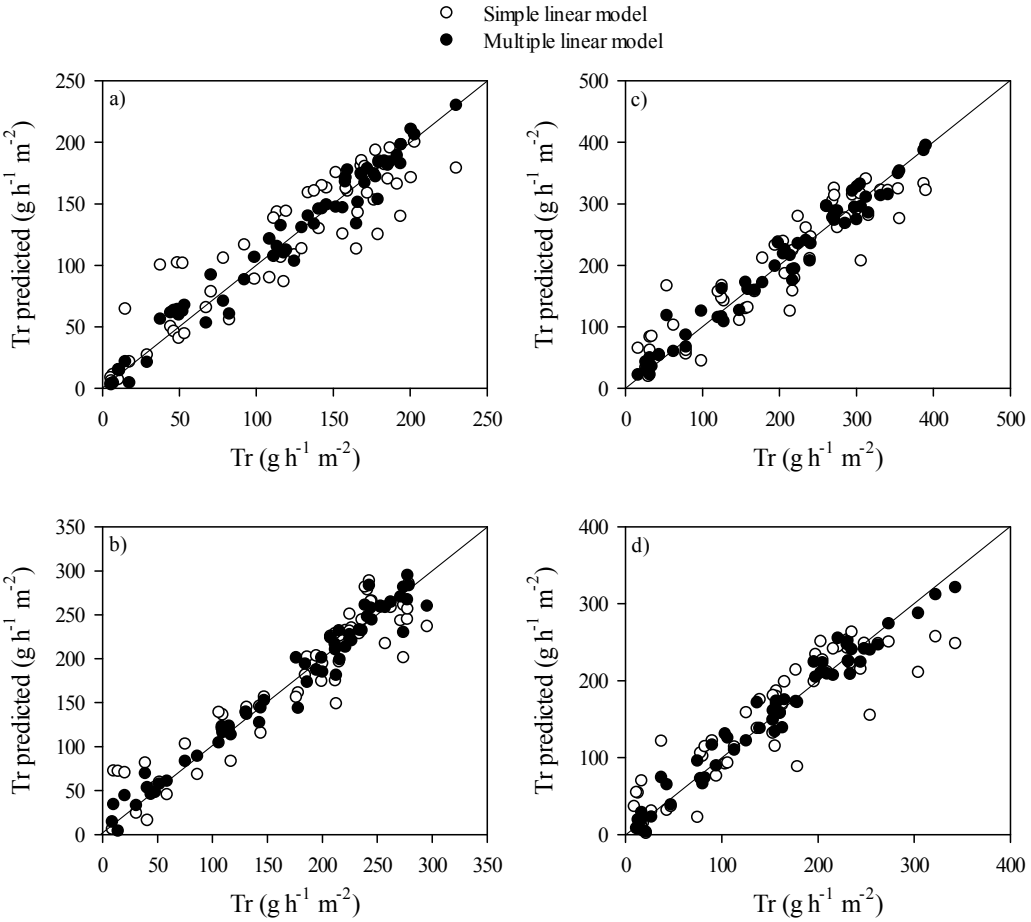


Figure 4. Relationship between transpiration measured (*Tr*) and predicted (*Tr* predicted) in *G. max* growing at the upslope (a and b) and footslope positions (c and d) in period 2 (a and c, DOY 211-215) and 3 (b and d, DOY 232-236) during 2011. See Table 2 for parameters, estimates and coefficients of determination. Straight line represents a 1:1 relationship and was included for reference.

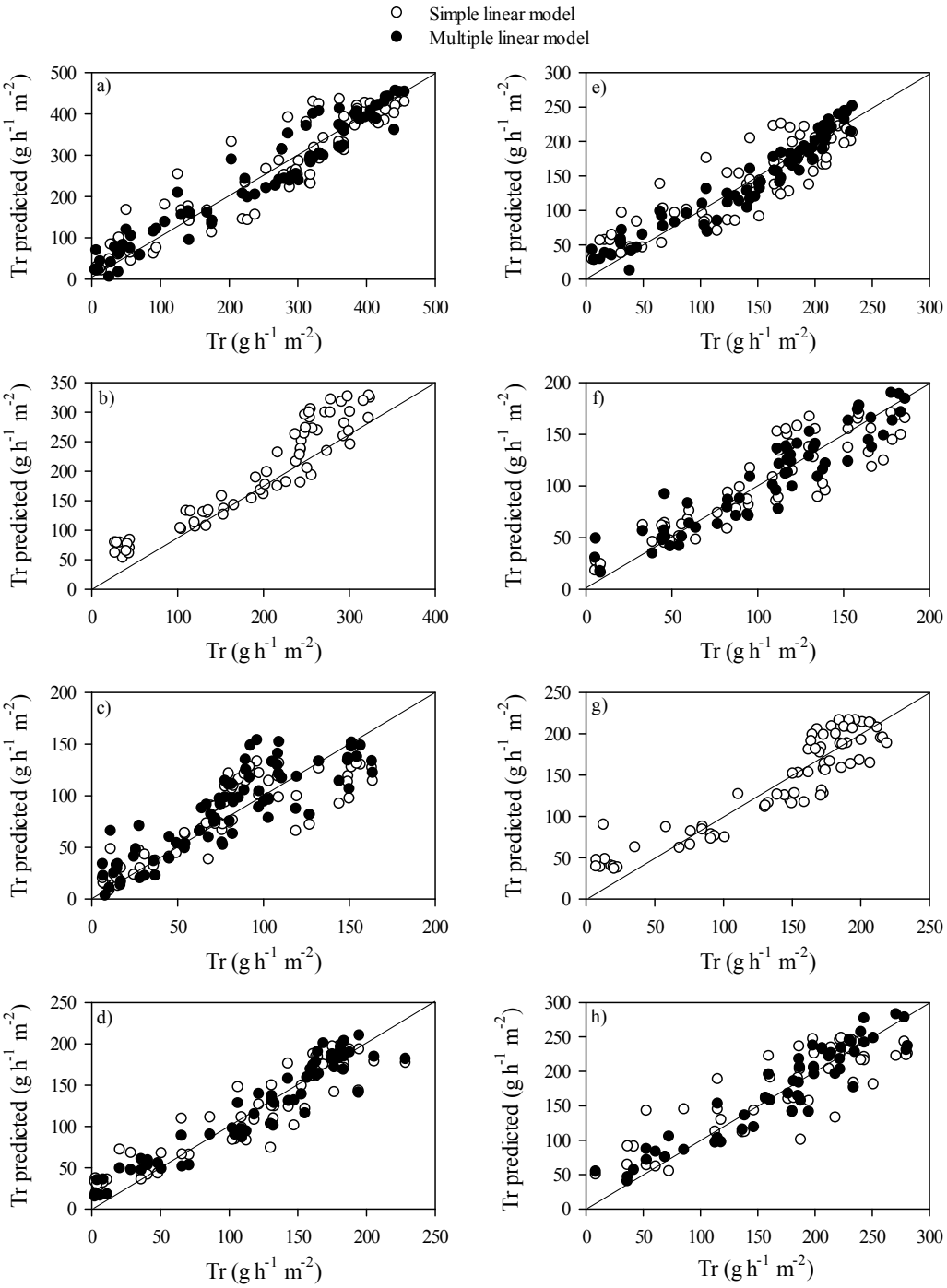


Figure 5. Relationship between transpiration measured (*Tr*) and predicted (*Tr* predicted) in *S. canadensis* growing at the upslope (a-d) and footslope positions (e-g) in period 1 (a and e, DOY 160-162, 164-166), 2 (b and f, DOY 188-189,192-194), 3 (c and g, DOY 213-216, 219-220) and 4 (d and h, DOY 252-256) during 2012. See Table 3 for parameters, estimates and coefficients of determination. Straight line represents a 1:1 relationship and was included for reference.

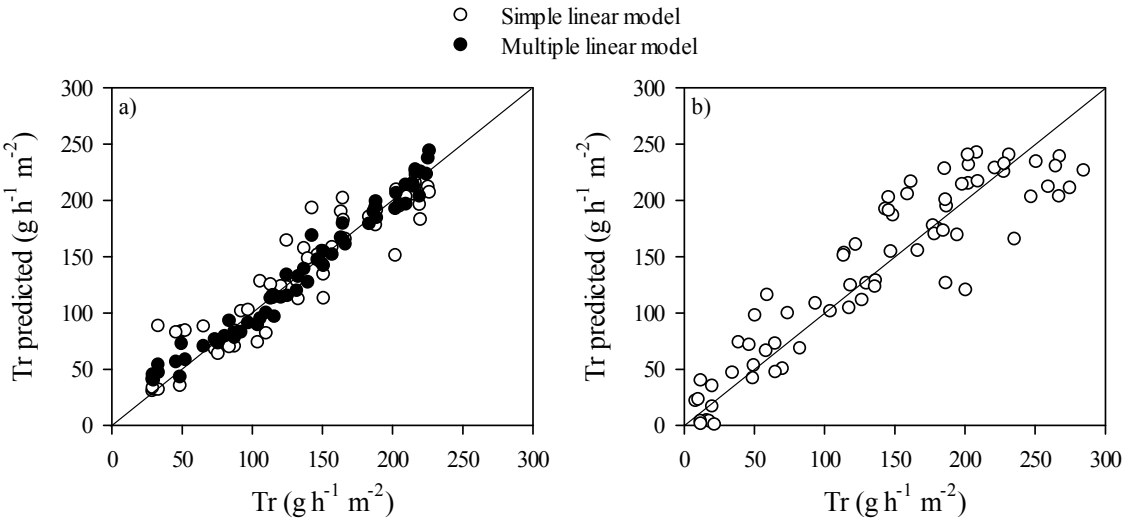


Figure 6. Relationship between transpiration measured (*Tr*) and predicted (*Tr* predicted) in *Z. mays* growing at the upslope position in period 2 (a, DOY 188-189, 192-194) and 3 (b, DOY 213-216 and 219-220) during 2012. See Table 3 for parameters, estimates and coefficients of determination. Straight line represents a 1:1 relationship and was included for reference.

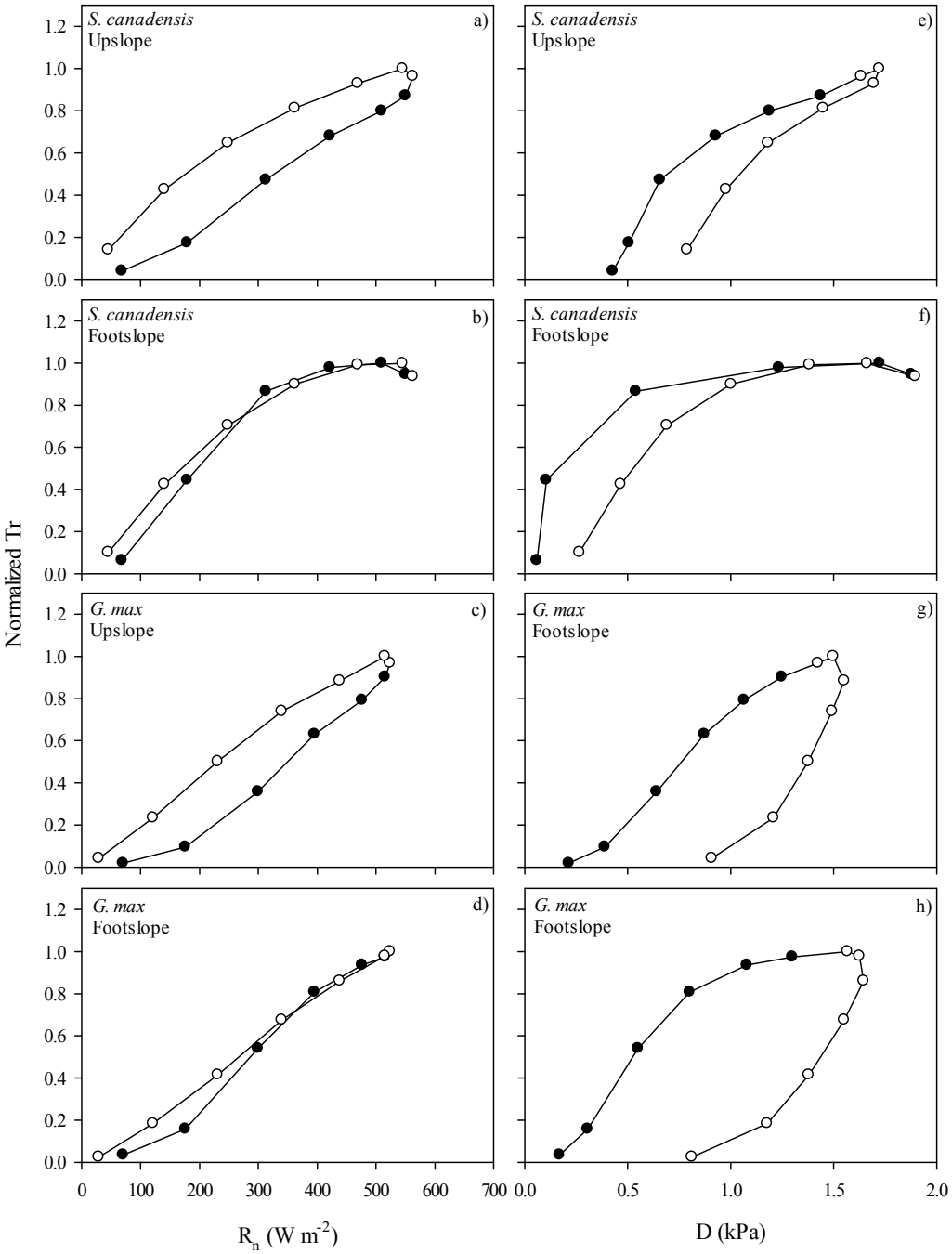


Figure 7. Relationship of normalized transpiration (*Tr*) with net radiation (*Rn*, left panel) and vapor pressure deficit (D_{ab}, right panel) for *S. canadensis* and *G. max* growing at the upslope and footslope positions in a mixed annual-perennial watershed in central Iowa. Each point represents an hourly value averaged over 5 days in 2011 (Period 2, DOY 211-215). Filled symbols correspond to morning (8:00 -13:00) and empty symbols stand for afternoon (14:00-20:00).

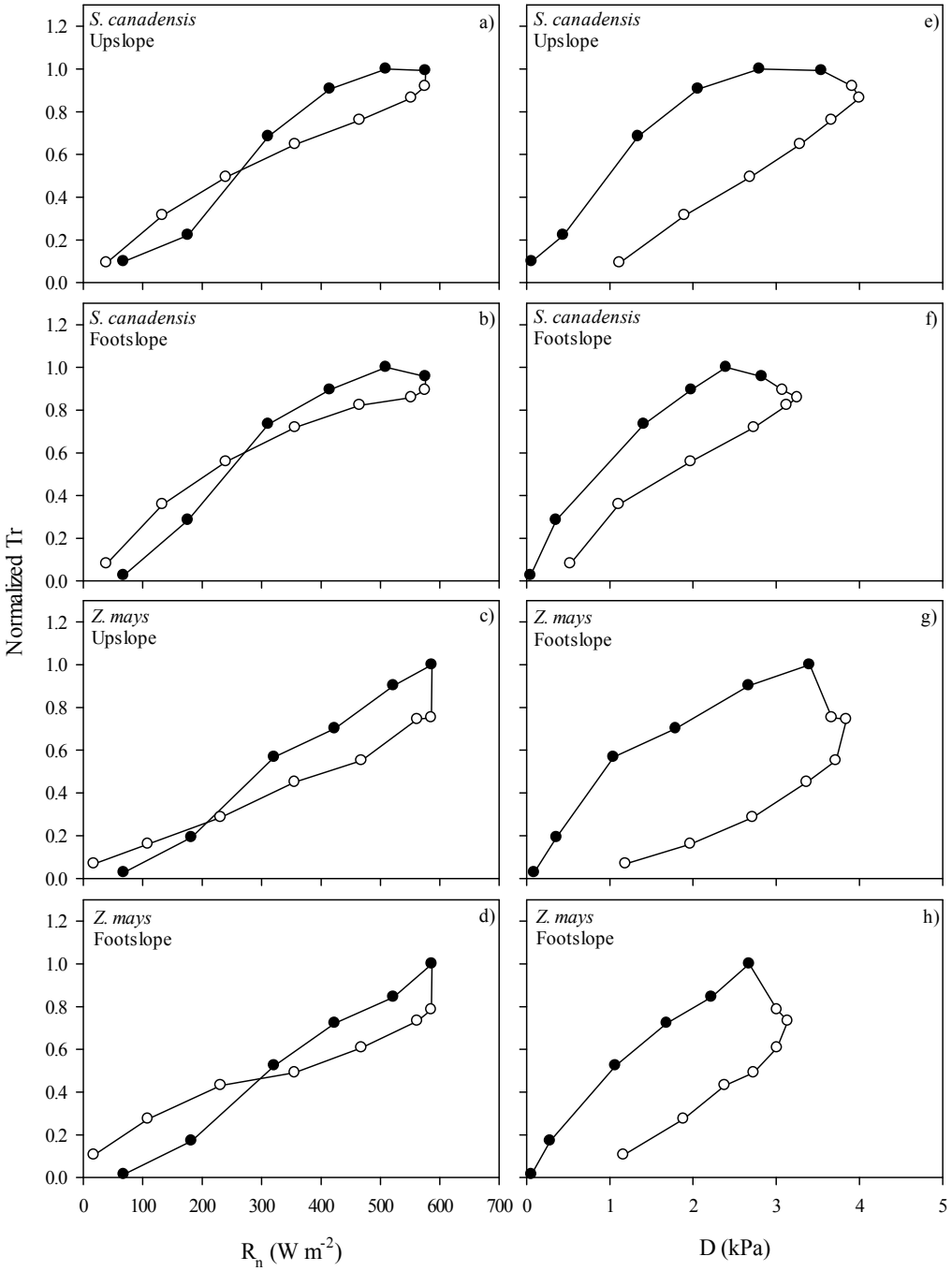


Figure 8. Relationship of normalized transpiration (*Tr*) with net radiation (*Rn*, left panel) and vapor pressure deficit (D_{ab}, right panel) for *S. canadensis* and *Z. mays* growing at the upslope and footslope positions in a mixed annual-perennial watershed in central Iowa. Each point represents an hourly value averaged over 5 days in 2012 (Period 3, DOY 213-216 and 219-220). Filled symbols correspond to morning (8:00 -13:00) and empty symbols stand for afternoon (14:00-20:00).

CHAPTER 4: IMPLICATIONS OF PLANT TRANSPIRATION IN THE HYDROLOGY OF A MIXED ANNUAL-PERENNIAL WATERSHED IN CENTRAL IOWA

A paper to be submitted to *Agriculture, Ecosystems & Environment*

Vilma S. Mateos-Remigio, Richard C. Schultz, Thomas J. Sauer, Heidi Asbjornsen

Abstract

Since the authorization of the Conservation Reserve Program by the Farm Bill in 1985, incorporation of native perennial strips at strategic locations within agricultural watersheds has been increasingly promoted in Iowa as a means to restore hydrologic processes severely damaged by intensive agriculture. The benefits of this conservation practice for reducing runoff, and nutrient and sediment export have already been documented, and the effects are commonly attributed to the high infiltration rates of soils under perennial vegetation. However, little attention has been given to understanding the potential impact that transpiration patterns of perennial species may have on regulating the hydrology of these watersheds managed under a mixed annual-perennial system. This study was conducted in an experimental watershed where 10% of the total area was covered with perennial vegetation distributed in strips at three topographic positions. The purpose was to provide information to elucidate the potential implications of transpiration patterns from perennial strips for on enhancing hydrological processes. Plant transpiration was measured in the dominant prairie species growing in the strips located at upslope and footslope positions

at different periods of the 2011 and 2012 growing seasons. Transpiration measurements were also collected from the adjacent crops. Whole-plant transpiration from *Solidago canadensis* (the most dominant prairie species) was scaled up from a 2 m^2 area of each strip sampled to approximate the contribution of this perennial species' transpiration to watershed evapotranspiration. Results showed higher transpiration in the strip at the upslope position than at the footslope position from July 8 to August 7 (2011) and from June 7 to July 12 (2012). This pattern was reversed for measurements collected between August 11-September 22 (2011) and July 20-September 13 (2012). Comparisons between the native prairie species and crops conducted when the latter were under full canopy conditions revealed that crop transpiration contributed a greater amount to total the watershed evapotranspiration than the native prairie species, at both topographic positions. Despite all the technical limitations and the complexity of the perennial strips, this study confirmed that plant transpiration from perennial strips may play an important role in reducing runoff by extracting more water from the soil in the early part of the growing season, when precipitation events are more frequent and soil water content is higher and that these hydrologic benefits outweigh the added technical and logistical complexities of managing mixed annual-perennial watersheds.

Introduction

In 1985, the Farm bill authorized the Conservation Reserve Program (CRP), which seeks to improve water quality and prevent soil erosion by planting perennial vegetation in place of crops, through different conservation practices such as riparian buffers, filter strips and contour grass strips (www.fsa.usda.gov). As part of this program, the incorporation of native perennial strips within agricultural dominated landscapes has been increasingly

promoted in Iowa, a state where the combined negative effect of intensive agriculture and extreme precipitation events are causing severe environmental degradation.

In recent years, a growing number of studies have demonstrated the diverse environmental benefits of planting strips of perennial vegetation at strategic locations within agricultural watersheds, specially related to hydrologic processess(Liebman et al., 2013; Asbjornsen et al., 2014), particularly in hydrological processes. Hernandez-Santana et al. (2013) showed that watersheds containing 10-20% of perennial vegetation exhibited up to 37% less surface runoff compared to watersheds that were 100% cropped. For the same study site, Zhou et al. (2014) found that nutrient concentration (nitrate-nitrogen, total nitrogen and total phosphorus) and export from surface runoff were significantly reduced in the mixed annual-perennial watersheds relative to watersheds without perennials. Similar benefits were observed when nitrate-nitrogen levels in the vadose zone and shallow groundwater were analyzed (Zhou et al., 2010). The reduced runoff and nutrient export from soils covered with perennial vegetation is generally attributed to its higher water infiltration rates compared to soils solely managed with annual crops. It has also been suggested that plant density in the vegetative strips slows down water flow velocity (Meyer et al., 1995) and blocks water flow and sediment (Ghadiri et al., 2001). Further, native prairie plants have been found to be more efficient than crops at retaining and stabilizing nitrogen in the soil (Perez-Suarez et al., 2014).

Plant transpiration is responsible for returning most of the soil water to the atmosphere and it is the largest component of the hydrological cycle (Schlesinger and Jasechko, 2014); therefore, it has a key role in the functioning of other hydrological processes such as runoff. However, relatively little is known about how water use by native

prairie species impacts the hydrology of landscapes managed under a mixed annual-perennial system. Studies comparing evapotranspiration (*ET*) between prairie ecosystems and corn/soybean fields suggest that the former may also help to reduce runoff not only because of higher soil water infiltration rates, but also because of high transpiration rates and total water use at specific times of the year. For example, although total seasonal or annual water use in prairie ecosystems is similar to that of crops, the former removes more water from the soil in the spring and late fall (Brye et al., 2000; Chapter 2 in this dissertation). Greater amounts of runoff and sediment export generally occur early in the growing season, which corresponds to the months of the year with highest soil water content due to snow melting and spring rain. The water removed from the soil by transpiration in spring may help increase soil water storage capacity later in the season. Another important feature of prairie species is their deep and extensive rooting structure, which enables them to access water from deeper soil layers resulting in lower water table levels relative to crop plants (Schilling and Jacobson, 2010). Quantifying the seasonal water use patterns of perennial plants within filter strips located in watersheds dominated by annual crops is critical to enhancing our understanding of the benefits of this conservation practice for improving watershed hydrology.

Measurements of water use in perennial filter strips must be made in small areas in order to generate meaningful information, which creates several highly complex challenges. Micrometeorological methods have the advantage of providing continuous data over long periods, but have a larger footprint than the typical size of the perennial strips; whereas at the other extreme, physiological techniques (transpiration at the leaf level) rely on instantaneous measurements. The Stem Heat Balance (SHB) technique, a thermometric method that

estimates whole-plant transpiration from sap flow measurements seems to be the most appropriate option, as it is suitable for small plants (Smith and Allen, 1996) and allows for continuous measurements of transpiration. Nevertheless, the SHB method also has some limitations, including the need to regularly rotate sensors to new plants to avoid damaging plant stems and compromising the accuracy of the data, which constrains us for determining seasonal patterns since measurements are taken on different plants throughout the season. On the other hand, scaling plant transpiration to the stand level in prairie vegetation becomes an extremely difficult task because of the diversity of the species and heterogeneity of plants distribution.

In this study, we address those challenges by taking intensive sap flow measurements for relatively short time periods (15-20 days) on small plots, assuming they were representative of the whole strips. Estimation of specific leaf area index (*LAI*) for the dominant species and by functional group was also necessary. Thus, this study represents the first attempt to provide information to elucidate the possible implications of transpiration patterns of perennials strips for enhancing hydrological processes in an agricultural landscape. We measured plant transpiration in the dominant native prairie species growing in strips located at two contrasting topographic positions in an experimental watershed, as well as in the adjacent crops, during different periods in the growing season of 2011 and 2012. We also measured *ET* to assess the contribution of species transpiration at the whole watershed level.

Materials and Methods

Study area

This research was conducted in a 3-ha experimental watershed located in the Neal Smith National Wildlife Refuge (NSNWR), which is situated in the Walnut Creek watershed in central Iowa (Figure 1). Climate is continental and humid, with an annual precipitation of 874 mm (30-year average, Midwestern Regional Climate Center, MRCC) and the highest monthly rainfall typically occurring in May and June (Schilling and Spooner, 2006).

About 90% of the watershed area is managed under an intensive no-till rotational corn-soybean system. The other 10% is covered by native perennial vegetation distributed in three contour strips (Figure 2): upslope (160 m length and 6.6 m width), sideslope (166 m length and 5.5 m width), and footslope (37 m length and 27 m width). These strips were planted in 2007 with a seed mix of tall grass prairie species, which were collected in the Refuge. The composition of the seed mix by weight was 27% grasses, 24% forbs, 5% weedy forbs and weedy grasses, and 44% inert matter (Hirsh et al., 2013). By 2011, the forb *Solidago canadensis* L. and two grasses (*Poa compressa* L. and *Poa pratensis* L.) were the most dominant species growing in the strips of 12 experimental watersheds located in the NSNWR (Hirsh et al., 2013), including the one used in this study.

Measurements, that will be described below, were taken during different periods of the growing seasons in 2011 and 2012 in prairie and crop plants (*Glyxine max* (L) Merr in 2011 and *Zea mays* L in 2012) growing in the upslope and footslope of the watershed (Figure 2), resulting in four study sites within the watershed: prairie upslope, crop upslope, prairie footslope and crop footslope.

Sap flow measurements

Whole-plant transpiration (*Tr*) [g h^{-1}] was estimated from sap flow measurements using the SHB technique. The theory of the method and equations are described extensively in Baker and van Bavel (1987). Sap flow gauges for stem diameters of 3, 5, 7, 19, and 25 mm were constructed in the laboratory following Senock and Ham (1993). Plots of 1 m^2 (1 m x 1m) were demarcated in the four study sites (Figure 2). Two plots were delimited in the perennial strips because vegetation is more heterogeneous and it was important to capture this variability during data collection. On the other hand, given that the strips contain a high diversity of species, we chose only the most dominant ones (usually 1 to 3 species) growing within the plots. Finally, a total of 10 plants per plot were selected for sap flow measurements. When more than one species was found to be dominant in the perennial plots, at least 3 individuals per species were sampled.

One gauge was placed on each plant at a minimum height of 10 cm above the ground to minimize errors induced by heat transfer from the soil (Weibel and Devos, 1994), and then gauges were wrapped with 3-cm-thick foam insulation and covered with aluminum foil to reduce errors due to radiation loading. Any leaves located on the stem segment below the gauge were removed and were not included when determining leaf area. Given that these leaves were located in the most shaded portion of the plant canopy, their removal was assumed to result in a negligible underestimation of whole-plant transpiration. A constant power system was used to supply energy to the gauges between 4:00 h and 21:00 h CST. Each gauge was connected to a cable (9537, Belden Inc., St. Louis, MO) and then to AM16/32 multiplexers and dataloggers (CR-10X and CR1000, Campbell Scientific Inc.,

Logan, UT). Signals from the gauges were sampled every 60 s and stored as 15-min averages.

Because the continuous energy supply may damage the plants and compromise accuracy of data, gauges had to be rotated to new plants regularly (approximately every 15-20 days). At the end of each measuring period, gauges were removed and plants were then harvested and brought to the laboratory to measure leaf area (LI-3100, LI-COR Bioscience, Lincoln, NE). Leaf area value from each plant was used to calculate sap flow on a leaf area basis that we will refer to as Tr_{leaf} hereafter [g h^{-1} m^{-2}].

LAI

The aboveground biomass from prairie plots was also collected at the end of each measuring period to determine leaf area. Plants were sorted to separate out the biomass of the species used for sap flow measurements, while the remaining biomass was separated into three functional groups: forbs, C_3 grasses and C_4 grasses. Identification of species was conducted using guides by Christiansen and Muller (1999), Kallenbach and Bishop-Hurley (2004), as well as information available on the internet. Identification at the species level was not always possible in some grasses. These "unknown" species were assigned to the C_3 grasses group, as well as all sedges and rushes. Each subsample was then separated into leaves, stems and dead material. Leaves were scanned in a leaf area meter to obtain estimates of *LAI* by dominant species and functional group.

Evapotranspiration and other micrometeorological measurements

A Bowen ratio energy balance system (BR) was installed near the crop upslope site to measure *ET*. Each system consisted of an air temperature/relative humidity probe (Model HMP45C, Vaisala Inc., Woburn, Mass., USA) and a thermistor. Sensors were mounted in aspirated radiation shields with a vertical separation of 1.5 m following the design of Bland et al. (1996) as adapted by Sauer et al. (2002). Sensor heights were adjusted as plant canopies developed to maintain the lower sensor about 0.5 m above the canopy. The sensors were exchanged every 5 min and this exchange mechanism was controlled by a CR23X datalogger (Campbell Scientific Inc., Logan, UT). Bowen ratio data were screened using criteria following Perez et al. (1999). Soil heat flux was measured with three heat flux plates (HFT1.1, Radiation and Energy Balance Systems) at a depth of 0.06 m. Plate values were corrected for heat storage in the 0 to 0.06-m soil layer (Sauer, 2002).

Other sensors were installed in the four study sites to measure different environmental parameters (Figure 2). Soil water content (θ) [m^3 m^{-3}] was measured with reflectometers (CS615, Campbell Scientific Inc., Logan, UT) positioned from 0 to 6 ($\theta_{0\text{-}6\ cm}$) and 6 to 20 cm depths (and $\theta_{6\text{-}20\ cm}$). Vapor pressure deficit (D) [kPa] was calculated as in Campbell and Norman (1998) from relative humidity (RH) [%] and air temperature (T_a) [°C] data that were collected at 2 m above the ground (HMP35C, Vaisala, Woburn, MA). Net radiation (R_n) [W m^{-2}] and wind speed (u) [m s^{-1}] were measured with a net radiometer (Q*7, Radiation and Energy Balance System, Seattle, WA) and a cup anemometer (014A cup anemometer, Met One, Grants Pass, OR), respectively, at 2 m above the soil surface only in the crop upslope and prairie footslope sites. All sensor signals were recorded every 10 s and stored as 15-min averages on CR23X dataloggers (Campbell Scientific Inc., Logan, UT). Electrical power was

supplied by deep cycle batteries (12 V) recharged by solar panels. Precipitation data were obtained from a station located approximately four km from our study area.

Sap flow scaling

We often failed to capture continuous data from all 10 plants sampled in each plot, especially in 2011, when we had more technical problems. This fact caused a reduction in the sample size that mainly affected our measurements in the prairie plots. Hence, we calculated average hourly and daily sap flow per species with the measurements of individuals from both plots in the perennial strips. Thus, the prairie species data used for further analysis were based on a 2 m^2 area.

Daily transpiration (T) [mm day^{-1}] in crop species was calculated by using the daily whole-plant Tr (F_d) [g day^{-1}] and the plant density (De) [plants ha^{-1}] (Bethenod et al., 2000; Sauer et al., 2007; Logsdon et al., 2014) in the following equation:

$$T = F_d \ \rho \ 10^3 De \ 10^{-10} \quad (1)$$

Where ρ is the density of water [g cm^{-3}] and the multipliers are unit conversion factors. From density surveys conducted, we found that *G. max*' *De* was 309000 and 303333 plants ha^{-1} at the upslope and footslope sites, respectively, whereas *De* in *Z. mays* was 69400 plants ha^{-1} at the upslope site and 67500 plants ha^{-1} at the footslope site. In canopies where plant size is not uniform, the plant sap flow should be normalized by leaf area and *De* is replaced by *LAI* as a scalar (Ham et al., 1990). Thus, daily T in prairie species was estimated by using daily Tr_{leaf} represented also as F_d [g m^{-2} day^{-1}] and unit conversion factors as follows:

$$T = F_d \ LAI \ 10^3 \ 10^{-6} \quad (2)$$

Gap filling

Due to datalogger and sap flow gauge malfunctioning, which occurred mainly in 2011, we missed data on some days. In Chapter 3 of this dissertation, we showed that *Rn* can be used as an hourly *Tr* predictor as it accounts for 79-89% of *Tr* variability. Therefore, we filled data gaps by using models created with data available from other days.

Data organization and analysis

We measured *Tr* and *LAI* in the perennial strips during 5 periods through the growing season in both years of study (Table 1). Data collection started later in 2011 because rainy conditions prevailed early in the growing season of that year. In period 1, 15 min-*Tr* rates were usually very small or zero throughout the day because the plants were also small. Therefore, we excluded period 1 from our analysis. The average leaf area of the plants used to determine Tr_{leaf} in the perennial plots is presented in Table 2. In the crops, *Tr* measurements were taken from period 3 (July 28 and June 23 in 2011 and 2012, respectively), when plants were strong enough to hold the gauges. The leaf area of the crop plants at the end of period 5 was not included in Table 2 because plants were almost senesced. However, we were able to estimate the crop's daily *T* for this period, because as was previously described, this is calculated from whole-plant *Tr*. Thus, we did not need sap flow on a leaf area basis in crops, which if used, would have overestimated our daily Tr_{leaf} in the first days of period 5.

For comparing water use by topographic position and species, we used Tr_{leaf} as this represents water use normalized by leaf area, which eliminates the effect of plant size. Statistical differences in daily Tr_{leaf} by topographic position and species in each period was

tested with the Mann-Whitney Rank Sum Test (p <0.5). To test differences we did not include days with predicted data (filled data). Thus, we selected only days when we had Tr_{leaf} obtained from direct measurements. Rainy days were always excluded from analysis because *Tr* is often overestimated or underestimated when gauges become wet.

Results and Discussion

Environmental conditions

Contrasting conditions among years were observed for precipitation (Figure 3a-b), $\theta_{0\text{-}6\text{ cm}}$ (Figure 3c-d), *D* (Fig. 3i-j), and somewhat for $\theta_{6\text{-}20\text{ cm}}$ (Figure 3e-f). In 2012, the year with lower rain amount, $\theta_{0\text{-}6\text{ cm}}$ was generally maintained below 0.2 m^3 m^{-3}, with the crop soil exhibiting the lowest water content. The $\theta_{0\text{-}6\text{ cm}}$ at prairie footslope was generally higher than at prairie upslope in both years. A similar trend was observed for the crop site in 2011 when there was data available for both sites (DOY 204-269). Surprisingly, $\theta_{0\text{-}6\text{ cm}}$ at crop footslope was usually lower than at crop upslope in 2012. The $\theta_{6\text{-}20\text{ cm}}$ was again higher at prairie footslope than at prairie upslope in 2011, but fairly similar between sites in 2012. In the crop sites, $\theta_{6\text{-}20\text{ cm}}$ was generally lower at the footslope position than at the upslope position in both 2011 and 2012.

LAI in prairie plots

Determining the *LAI* in the prairie plots was important not only for scaling up purposes, but it also allowed us to identify the seasonal and inter-annual changes in vegetation. Table 3 shows the total *LAI* in the plots sampled, *LAI* for specific groups, and also for *S. canadensis*, which was the most dominant species throughout the growing season

in both years of study. In the 2011 growing season, total *LAI* ranged from 0.9 to 3.16 at the upslope position (average = 1.90), and from 0.52 to 5.03 at the footslope position (average = 2.49). In 2012, *LAI* values were generally smaller: 0.59 to 2.08 at upslope (average = 1.41), and 1.08 to 2.72 at footslope slope (average = 1.84). Similar to our findings, Nippert et al. (2011) observed higher *LAI* in lowland plots compared to those in the upland in a native tallgrass prairie located within the Konza Prairie Biological Station in Kansas. In their study, *LAI* ranged from ~ 1 to 4 in the upland and from ~ 1 to 6 in the lowland plots throughout the growing season. Lower maximum values in our study are reasonable because the prairie strips were only 7 years old.

Studies assessing biomass (another growth index) along topographic gradients in tallgrass prairies have found it to be lower in upland positions relative to contrasting topographic positions (Briggs and Knapp, 1995, Dornbush and Wilsey, 2010). This result has been attributed to greater soil depth, higher soil water content and higher nutrient availability in the lowlands. Thus, these soils are able to support more biomass (Dornbush and Wilsey, 2010). In this study, $\theta_{0\text{-}6\ cm}$ was generally higher in the prairie footslope plot during both 2011 and 2012 (Figure 3c-d), while differences were less evident at 6-20 cm depth (Figure 3e-f), especially in 2012 (Fig. 3f). Therefore, we suggest that $\theta_{0\text{-}6\ cm}$ determined, at least partially, the *LAI* dissimilarity among topographic positions. The same premise can be used to explain lower *LAI* in 2012 compared to 2011.

The average contribution of *S. canadensis* to the total *LAI* during the whole growing season was similar among topographic positions in both years: 42.4% and 42.0% (2011), and 65.0% and 66.8% (2012) at the upslope and footslope positions, respectively. Adding *S. canadensis* and the other forbs together, their average contribution to growing season *LAI* in

2011 was 64.0% at the prairie upslope position and 76.5% at the footslope position, the C_3 grasses were 17.8% (prairie upslope) and 14.5% (prairie footslope), and C_4 grasses were 18.0% (prairie upslope) and 9.1% (prairie footslope). For 2012 growing season, all forbs represented an average of 72.6% and 84.3% of the total *LAI* at the upslope and footslope positions, respectively; whereas C_3 grasses average contribution was 17.5% (prairie upslope) and 14.2 % (prairie footslope), and C_4 grasses were 10% (prairie upslope) and 1.3% (prairie footslope) of the total *LAI*. These results also show that *S. canadensis* was even more dominant in the dry year.

Nolf et al. (2014) showed that *S. canadensis* has physiological traits (i.e. stomatal regulation and hydraulic architecture) that confer a high degree of hydraulic plasticity, and hence, increases its colonizing potential. This characteristic may, in part, explain the dominance of this species in our prairie strips. Although other forbs such as *Ratibida pinnata* (Vent.) Barnhart and *Monarda fistulosa* L. may represent a relevant proportion of total *LAI*, they were not always present in the sampled plots.

It was interesting to find that C_4 grasses' *LAI* was substantially reduced in the dry year, while *S. canadensis*, the dominant C_3 forb, exhibited an increase in *LAI*. Larger sensitivity of C_4 grasses to soil moisture was previously reported by Briggs and Knapp (1995). They suggested that a decline in soil moisture impacted grass productivity negatively, and that forbs took advantage of the reduced competition. Conversely, Hoover et al. (2014) found that forb biomass (particularly *S. canadensis*) experienced a greater reduction than C_4 grasses after a 2-years-drought. They attributed that result to soil water depletion that may have occurred in deeper soil layers that C_3 species relied on for water uptake. In our study, it is likely that the drought intensity in 2012 was not enough to drastically impact the θ at

layers deeper than 20 cm. Thus, forbs, represented by *S. canadensis*, were able to sustain their productivity. In addition, the hydraulic acclimation of this species that was described by Nolf et al. (2014) may have also helped to increase its contribution to total *LAI* on that year.

Daily Tr_{leaf} comparison by topographic position

Because *S. canadensis* was the most dominant species, we focused our comparative analysis between this species and the crops. In 2011, we were able to make comparisons between topographic positions for *S. canadensis* only during period 3, 4 and 5 (Figure 4b-d). Significant differences were found in periods 3 (Figure 4b) and 4 (Figure 4c). In period 3, daily Tr_{leaf} was significantly higher in the upslope position than in the footslope position (p = 0.041), and the opposite was found in period 4 (p = 0.001). In 2012, we had a more complete data set and we present results for four periods (Figure 4e-h). Significant differences were found in periods 2, 3 and 4 (Figure 4f-h).

Given that θ is generally higher in lowland positions, we expected daily Tr_{leaf} would be constantly higher in the footslope site. Turner and Knapp (1996) recorded monthly stomatal conductance on *Solidago spp*. at upland and lowland positions, and found that stomatal conductance averaged over the growing season was higher in the lowland. In our study we observed a trend of higher daily Tr_{leaf} at the upslope position in periods 2 and 3, and lower in periods 4 and 5. The disagreement between our results with those of Turner and Knapp (1996) may be due to the effect of light competition that was not a limiting factor in their study as measurements were taken on top leaves that were well exposed to light. When measurements are taken at the whole-plant level, other factors such as plant competition and its consequent effect on light conditions may play a role in the seasonal changes of water use,

in addition to the effects of θ. Our *LAI* results support this premise. The contribution of *S. canadensis' LAI* to total *LAI* in periods 2 and 3 was higher at the upslope position compared to the footslope position in both years of study (47.8% and 30.3% vs. 15.9% and 20.3 %, in 2011; 69.8% and 82.9% vs. 49.0% and 76.5% in 2012, Table 3). This suggests that at upslope position, species competition may have been lower and more light was available for *S. canadensis.* In contrast, at the footslope position, other species represented an important portion of total *LAI*. For example in 2011, leaf area of other forbs (period 2) and C_3 grasses (period 3) occupied 70.7 % and 46.6% of the area, respectively. Therefore, a reduced light availability for *S. canadensis* may have been responsible for lower transpiration at the lowland position. In periods 3 and 4 in both 2011 and 2012, *LAI* of *S. canadensis* at the upslope position was similar or lower than at the footslope position. Thus, *S. canadensis*' Tr_{leaf} at the upslope position might have been limited not only by higher light competition with other species, but also by the longer water stress that plants were subjected to, relative to the plants growing in the footslope position.

In crops, we sampled three periods (3, 4, and 5) in both years, but we used data only from periods 3 and 4 for paired comparisons. When plants were collected at the end of period 5, they were almost senesced, so that the total leaf area measured on living leaves was low which resulted in overestimation of Tr_{leaf} at the beginning of the period. In *G. max*, the crop in 2011, daily Tr_{leaf} at the footslope position was higher than at the upslope position during period 3 ($p = 0.050$, Figure 5a); whereas in period 4, plants at the upslope position exhibited higher Tr_{leaf} ($p = 0.026$, Figure 5b). The daily water use patterns among periods might also be explained by the effect of shading among individuals. In period 3, we found *LAI* was higher at the upslope position (5.15) than at the footslope position (4.69). The opposite was recorded

in period 4 (3.13 and 4.43 at upslope and footslope position, respectively). Fay and Knapp (1998) reported that *G. max* leaves showed a rapid stomatal conductance closure when leaves were exposed to shade. We did not find significant differences in daily Tr_{leaf} by topographic position for *Z. mays*, the 2012 crop (Figure 5c-d).

Daily Tr_{leaf} comparison by species

Figure 6a-b show comparisons of daily Tr_{leaf} between *S. canadensis* and *G. max* growing at upslope positions during periods 3 and 4, respectively; whereas Figure 6c-d compare daily Tr_{leaf} in *S. canadensis* and *Z. mays*. In period 3 of both 2011 and 2012, we found that daily Tr_{leaf} of *S. canadensis* was significantly higher than in the crops (Figure 6a and c). On the contrary, in period 4, lower daily Tr_{leaf} was observed for *S. canadensis* (Figure 6b and d). This consistent shift from period 3 to 4 may be the result of phenological differences among the perennial and the crop species. While in period 4 both crops were in the reproductive stage (pod and grain filling for *G. max* and *Z. mays*, respectively), when their water requirements are usually highest (Dogan et al., 2007; Martins da Silva et al., 2009); *S. canadensis* was entering the flowering stage. Interestingly, we did not find significant differences in daily Tr_{leaf} among species at the footslope position in either year of the study (Figure 7a-d). Although we did not find a convincing explanation for this result, we hypothesize that in the lowland position where $\theta_{0\text{-}6\ cm}$ was higher in the prairie strip relative to the crop area, *S. canadensis* might have been able to sustain transpiration rates similar to those of the crops.

Daily *T* contribution to *ET*

The scaled sap flow data in the perennial species and crops were used to provide an estimation of the daily *T* contribution to watershed *ET*. Due to technical problems with the temperature sensors in our *BR* system in 2012, *ET* measurements were suspiciously low. To approximate the contribution of daily *T* in that year, we used *ET* data measured by Hernandez-Santana et al. (In prep.) using an Eddy Covariance (EC) system in a watershed located approximately four km from our study site. To verify whether using *ET* from another site and measured with another technique would have a significant impact in our final assessment for 2012, we compared daily *T* measured with BR and EC during the periods of measurements in 2011 (data not shown). The student's t-tests showed that there was no statistical difference in average daily *ET* among sites ($p > 0.05$). In fact means in each period were quite similar.

In a study conducted in 2008 (Chapter 2) we estimated *Z. mays*' *T* on a daily basis from sap flow data and reasonable results were obtained as the one month-average daily *T* was 89% of *ET*. The other 11% was attributed to soil water evaporation. In the same study, we tried to scale up sap flow from prairie species to the stand level. However, daily *T* was overestimated because *LAI* was not determined by species but by functional group (C_3 forbs and C_4 grasses). Based on that experience, in this study, we calculated the specific *LAI* for the dominant species in the prairie strips.

The cumulative *T* for every period is presented in Table 4. For 2011, we found that *S. canadensis'* cumulative *T* at the upslope position represented between 19.4 % (period 4) and 62.6% (period 3) of the cumulative *ET*, whereas at the footslope position, cumulative *T* ranged from 23.0% (period 5) to 54.4% (period 3) of the cumulative *ET* in periods 3-5. In

2012, cumulative *T* at the upslope position was between 27.1% (period 4) and 82.8% (period 2) of *ET*. At the footslope position, the contribution of *T* to *ET* ranged from 32% (period 2) to 69.6% (period 5). Our cumulative *T* results are in agreement with the *LAI* and daily Tr_{leaf} trends *of S. canadensis* over the growing season. Higher water loss occurred at the upslope position in periods 2 and 3 when both Tr_{leaf} and *LAI* of *S. canadensis* were higher than in periods 4 and 5. During periods 4 and 5, daily Tr_{leaf} and *LAI* of *S. canadensis* were higher in the footslope position, and hence, cumulative *T* was also higher relative to the upslope position.

The cumulative *T* in *G. max* during period 3 and 4 was higher than *ET* by 3% and 19.5 % at upslope position, and by 29% and 20% at footslope position. In contrast, daily *Z. mays' T* was always lower than *ET*, as expected. The cumulative *T* at upslope position was 70.1 %, 59.9%, and 39.7% of *ET* for periods 3, 4 and 5 respectively. At the footslope position, cumulative *T* was 80.8%, 92.9%, and 31.02% of *ET*.

Overestimation of *T* that has been calculated from sap flow measurements has been reported in previous studies with *G. max*, Z. *mays* and *Gossypium hirsutum* (L) (Ham et al., 1990; Gerdes et al., 1994; Logsdon et al., 2014), and it has been attributed to different causes such as plant size variability across the crop field (Ham et al., 1990; Logsdon et al., 2014) and errors associated with the gauge design (Gerdes et al., 1994). Conversely, Sauer et al (2010) found good agreement between daily *T* and *ET*. They reported that *G. max'* daily *T* contribution to *ET* was 88% and 92% on two days used to represent full canopy conditions ($LAI > 4$). It is not clear why our calculated crop *T* was overestimated only during the year with *G. max*.

One initial goal of this study was to determine the total seasonal *T* in the perennial strips to elucidate its actual impact on the hydrology of the watershed. We scaled up *S. canadensis* daily Tr_{leaf} using the *LAI* from the forbs group, and while the result was reasonable in some periods because the daily *T* was less than *ET*, in other periods *T* was overestimated. We attribute this result to the differences in transpiration rates among species even from the same functional group. Thus, the extremely high diversity of species in the perennial strips made this goal impossible to achieve.

Implications for watershed hydrology

To fully understand the impact of perennial strips on watershed hydrology from a plant water use perspective, daily and seasonal transpiration would have to be estimated at the stand level. However, the high diversity of species in the strips (which constrains the scaling of transpiration from the plant to the stand level) in addition to the restrictions imposed by the method used to measure plant transpiration (which requires to rotate sensors to new plants regularly to avoid damage on the stems and compromise the accuracy of the data) limits us from drawing conclusive statements from the results of the study. However, the results have helped to enhance our knowledge of water use by some perennial and annual crop plants growing in different landscape positions.

We found a consistent pattern in *LAI* and daily Tr_{leaf} for *S. canadensis* in both years of study, which suggested that in our 2 m^2 plots, higher *T* occurs at prairie upslope position until July-August and in the following months *T* at prairie footslope position becomes greater. Assuming that the results from the plots are representative of the whole strips, we suggest that *S. canadensis T* in the upslope strip may contribute to increased soil water storage

capacity in the first half of the growing season, and this could have positive impacts on the reduction of surface runoff from adjacent annual crop fields.

Collection of *Tr* data started later on the crops because plants were very small when *S. canadensis* plants were already able to hold the sap flow gauges. This confirms that the longer growing season of perennial species enables them to extract water from the soil earlier in the growing season when it is most needed because more rainfall occurs in the spring and early summer in much of the Corn-belt of the Midwestern United States. Our cumulative *T* for the perennial species and crops during periods 3 and 4 agree with previous findings, which show that during the middle of growing season, crop *ET* is usually higher than that prairie plants. This suggests that the potential positive impact of perennial's water use to help reduce surface runoff is valuable at the beginning and end of the growing season.

Acknowledgements

This research was supported by the Iowa State University's College of Agriculture and Life Sciences; the Leopold Center for Sustainable Agriculture; the U.S. Department of Agriculture's National Research Initiative, Agriculture and Food Research Initiative, and Sustainable Agriculture Research and Education programs; and the U.S. Forest Service. We thank Forrest Goodman, Chris Witte, Gabriela Lopez-Flores and Omar de Kok-Mercado for their help in deploying the equipment used during this research and collecting the data.

References

Asbjornsen, H., Shepherd, G., Helmers, M.,Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern US. Plant and Soil. 308(1-2), 69-92.

Baker, J.M.,van Bavel, C.H.M., 1987. Measurement of mass flow of water in the stems of herbaceous plants. Plant Cell Environ. 10(9), 777-782.

Bethenod, O., Katerji, N., Goujet, R., Bertolini, J.M.,Rana, G., 2000. Determination and validation of corn crop transpiration by sap flow measurement under field conditions. Theor. Appl. Climatol. 67(3-4), 153-160.

Bland, W.L., Loew, J.T.,Norman, J.M., 1996. Evaporation from cranberry. Agric. For. Meteorol. 81(1-2), 1-12.

Briggs, J.M.,Knapp, A.K., 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. Am. J. Bot. 82(8), 1024-1030.

Brye, K.R., Norman, J.M., Bundy, L.G.,Gower, S.T., 2000. Water-budget evaluation of prairie and maize ecosystems. Soil Sci. Soc. Am. J. 64(2), 715-724.

Campbell, G.S.,Norman, J.M., 1998. An Introduction to Environmental Biophysics. Springer, New York.

Christiansen, P.,Muller, M., 1999. An illustrated guide to Iowa prairie plants. University of Iowa Press, Iowa City, 240 pp.

Dogan, E., Kirnak H., Copur O., 2007. Deficit irrigations during soybean reproductive stages and CROPGRO-soybean simulations under semi-arid climatic conditions. Field Crops Res. 103(2), 154-159.

Dornbush, M.E.,Wilsey, B.J., 2010. Experimental manipulation of soil depth alters species richness and co-occurrence in restored tallgrass prairie. J. Ecol. 98(1), 117-125.

Gerdes, G., Allison, B.E.,Pereira, L.S., 1994. Overestimation of soybean crop transpiration by sap flow measurements under field conditions in central Portugal. Irrigation Sci. 14(3), 135-139.

Ghadiri, H., Rose, C.W.,Hogarth, W.L., 2001. The influence of grass and porous barrier strips on runoff hydrology and sediment transport. Trans. ASAE. 44(2), 259-268.

Ham, J.M., Heilman, J.L.,Lascano, R.J., 1990. Determination of soil water evaporation and transpiration from energy balance and stem flow measurements. Agric. For. Meteorol. 52(3-4), 287-301.

Hernandez-Santana, V., Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R.,Tomer, M., 2013. Native prairie filter strips reduce runoff from hillslopes under annual row-crop systems in Iowa, USA. J. Hydrol. 477, 94-103.

Hirsh, S.M., Mabry, C.M., Schulte, L.A.,Liebman, M., 2013. Diversifying agricultural catchments by incorporating tallgrass prairie buffer strips. Ecol. Restor. 31(2), 201-211.

Hoover, D.L., Knapp, A.K.,Smith, M.D., 2014. Resistance and resilience of a grassland ecosystem to climate extremes. Ecology. 95(9), 2646-2656.

Kallenbach, R.,Bishop-Hurley, G.J., 2004. A guide to the common forages and weeds of pastures. University of Missouri, Missouri, 52 pp.

Liebman, M., Helmers, M.J., Schulte, L.A.,Chase, C.A., 2013. Using biodiversity to link agricultural productivity with environmental quality: Results from three field experiments in Iowa. Renewable Agric. Food Syst. 28(2), 115-128.

Logsdon, S.D., Singer, J.W., Prueger, J.H.,Hatfield, J.L., 2014. Comparison of corn transpiration, Eddy covariance, and soil water loss. Soil Sci. Soc. Am. J. 78(4), 1214-1223.

Martins da Silva, M., Libardi P.L., Silva F.C., 2009. Nitrogen doses and water balance components at phenological stages of corn. Sci. Agric. 66(4), 515-521.

Meyer, L.D., Dabney, S.M.,Harmon, W.C., 1995. Sediment-trapping efectivenes of stiff-grass hedges. Trans. ASAE. 38(3), 809-815.

Nippert, J.B., Ocheltree, T.W., Skibbe, A.M., Kangas, L.C., Ham, J.M., Arnold, K.B.S.,Brunsell, N.A., 2011. Linking plant growth responses across topographic gradients in tallgrass prairie. Oecologia. 166(4), 1131-1142.

Nolf, M., Pagitz, K.,Mayr, S., 2014. Physiological acclimation to drought stress in *Solidago canadensis*. Physiol. Plantarum. 150(4), 529-539.

Perez-Suarez, M., Castellano, M.J., Kolka, R., Asbjornsen, H.,Helmers, M., 2014. Nitrogen and carbon dynamics in prairie vegetation strips across topographical gradients in mixed Central Iowa agroecosystems. Agr. Ecosyst. Environ. 188, 1-11.

Perez, P.J., Castellvi, F., Ibanez, M.,Rosell, J.I., 1999. Assessment of reliability of Bowen ratio method for partitioning fluxes. Agric. For. Meteorol. 97(3), 141-150.

Sauer, T.J., Moore, P.A., Ham, J.M., Bland, W.L., Prueger, J.H.,West, C.P., 2002. Seasonal water balance of an Ozark hillslope. Agric. Water Manage. 55(1), 71-82.

Sauer, T.J., Singer, J.W., Prueger, J.H., DeSutter, T.M.,Hatfield, J.L., 2007. Radiation balance and evaporation partitioning in a narrow-row soybean canopy. Agric. For. Meteorol. 145(3-4), 206-214.

Schilling, K.E.,Jacobson, P., 2010. Groundwater conditions under a reconstructed prairie chronosequence. Agr. Ecosyst. Environ. 135(1-2), 81-89.

Schilling, K.E.,Spooner, J., 2006. Effects of watershed-scale land use change on stream nitrate concentrations. J. Environ. Qual. 35(6), 2132-2145.

Schlesinger, W.H.,Jasechko, S., 2014. Transpiration in the global water cycle. Agric. For. Meteorol. 189, 115-117.

Senock, R.S.,Ham, J.M., 1993. Heat balance sap flow gauge for small diameter stems. Plant Cell Environ. 16(5), 593-601.

Smith, D.M.,Allen, S.J., 1996. Measurement of sap flow in plant stems. J. Exp. Bot. 47(305), 1833-1844.

Turner, C.L.,Knapp, A.K., 1996. Responses of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology. 77(6), 1738-1749.

Weibel, F.P.,Devos, J.A., 1994. Transpiration measurements on apple trees with an improved stem heat balance method. Plant and Soil. 166(2), 203-219.

Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R.,Tomer, M.D., 2010. Perennial filter srips reduce nitrate levels in soil and shallow groundwater after grassland-to-cropland conversion. J. Environ. Qual. 39(6), 2006-2015.

Zhou, X., Helmers, M.J., Asbjornsen, H., Kolka, R., Tomer, M.D.,Cruse, R.M., 2014. Nutrient removal by prairie filter strips in agricultural landscapes. J. Soil Water Conserv. 69(1), 54-64.

Table 1. Day of year (DOY) and its corresponding date for the periods when leaf area index (*LAI*) and sap flow were measured in 2011 and 2012.

	2011		2012	
Period	DOY	Date	DOY	Date
1	160 - 172	Jun 9 - Jun 21	135 - 142	May 14 - May 21
2	189 - 199	Jul 8 - Jul 18	159 - 169	Jun 7 - Jun 17
3	209 - 219	Jul 28 - Aug 7	175 - 194	Jun 23 - Jul 12
4	233 - 243	Aug 11 - Aug 31	201 - 221	Jul 20 - Aug 8
5	248 - 265	Sep 5 - Sep 22	238 - 257	Aug 24 - Sep 13

Table 2. Average leaf area per plant from the plants sampled with sap flow sensors at the end of each measurement period in 2011 and 2012.

Period	Species	Leaf area (m^2) 2011		Leaf area (m^2) 2012	
		Upslope site	Footslope site	Upslope site	Footslope site
2	*S. canadensis*	0.052 ± 0.005		0.019 ± 0.003	0.060 ± 0.004
3	*S. canadensis*	0.060 ± 0.002	0.095 ± 0.014	0.036 ± 0.004	0.069 ± 0.006
	G. max	0.146 ± 0.014	0.140 ± 0.018		
	Z. mays			0.366 ± 0.010	0.468 ± 0.024
4	*S. canadensis*	0.066 ± 0.005	0.071 ± 0.011	0.029 ± 0.005	0.063 ± 0.007
	G. max	0.101 ± 0.012	0.122 ± 0.010		
	Z. mays			0.270 ± 0.040	0.359 ± 0.030
5	*S. canadensis*	0.029 ± 0.004	0.051 ± 0.008	0.027 ± 0.006	0.030 ± 0.003

Table 3. Leaf area index (*LAI*) at the end of each measuring period in 2011 and 2012 in the perennial plant strips of a mixed annual-perennial watershed in central Iowa.

Species/Group	Position	*LAI* 2011					*LAI* 2012				
		Period 1	Period 2	Period 3	Period 4	Period 5	Period 1	Period 2	Period 3	Period 4	Period 5
S. canadensis	Upslope	0.221	1.066	0.957	0.625	0.755	0.221	1.131	1.335	1.569	0.455
	Footslope	0.847	0.521	1.023	0.761	0.436	0.699	0.882	2.080	1.641	0.903
Other forbs	Upslope	0.104	0.651	0.880	0.719	0.063	0.104	0.249	0.027	0.245	
	Footslope	1.030	2.319	0.529	0.456	0.060	0.687	0.362	0.034	0.363	0.029
C_3 grasses	Upslope	0.477	0.332	0.292	0.447	0.013	0.476	0.149	0.245	0.173	0.076
	Footslope	0.118	0.192	2.342	0.207	0.007	0.118	0.442	0.610	0.085	0.132
C_4 grasses	Upslope	0.338	0.183	1.030	0.254	0.065	0.333	0.094		0.097	0.059
	Footslope		0.245	1.138	0.189	0.019		0.093			0.015
Total	Upslope	1.14	2.23	3.16	2.05	0.90	1.13	1.62	1.61	2.08	0.59
	Footslope	1.995	3.28	5.03	1.61	0.52	1.50	1.80	2.72	2.09	1.08
S. canadensis % of total *LAI*	Upslope	19.38	47.8	30.3	30.5	83.9	19.6	69.8	82.9	75.4	77.1
	Footslope	42.46	15.9	20.3	47.3	83.8	46.6	49.0	76.5	78.5	83.6

Table 4. Cumulative evapotranspiration (*ET*) and transpiration (*T*) in *S. canadensis*, *G. max*, and *Z. mays* for each measurement period in 2011 and 2012. Rainy days were excluded. In 2012, daily *ET* was missed on some days in period 3 (DOY 182), period 4 (DOY 202 and 2010) and period 5 (DOY 242). These days were also excluded from the cumulative *T*.

2011					
Period	*ET* (mm)	*T* (mm)			
		S. canadensis Upslope	*S. canadensis* Footslope	*G. max* Upslope	*G. max* Footslope
2	50.4	26.1			
3	42.2	26.4	23.0	43.7	54.6
4	82.2	15.9	22.9	98.2	98.5
5	48.5	17.4	11.2		

2012					
Period	*ET* (mm)	*T* (mm)			
		S. canadensis Upslope	*S. canadensis* Footslope	*Z. mays* Upslope	*Z. mays* Footslope
2	42.3	35.0	13.5		
3	103.7	64.4	54.1	72.7	83.8
4	92.8	25.2	46.6	55.6	86.2
5	43.7	12.0	30.4	17.4	13.6

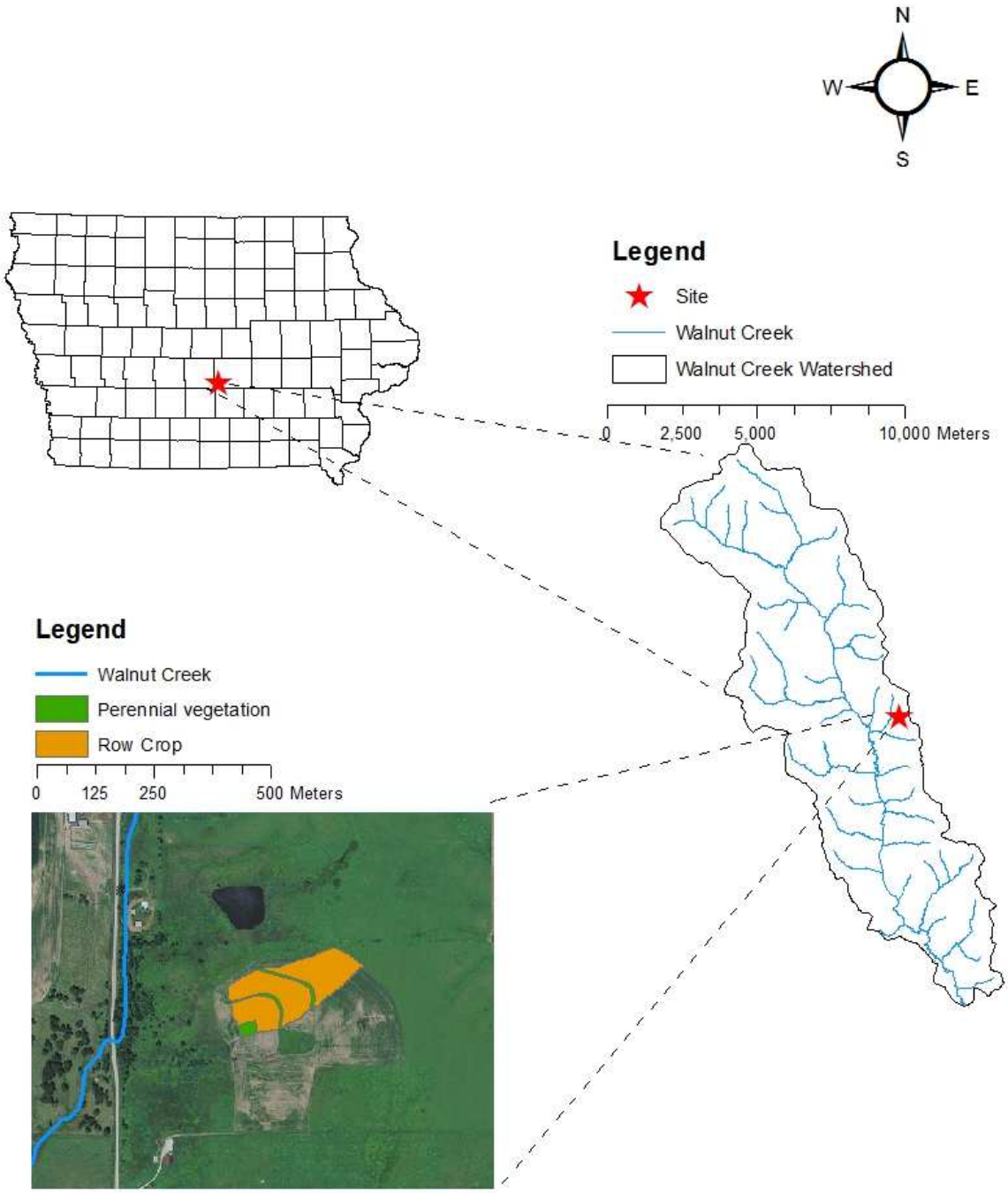


Figure 1. Location of the mixed annual-perennial watershed within the Walnut Creek watershed in central Iowa.

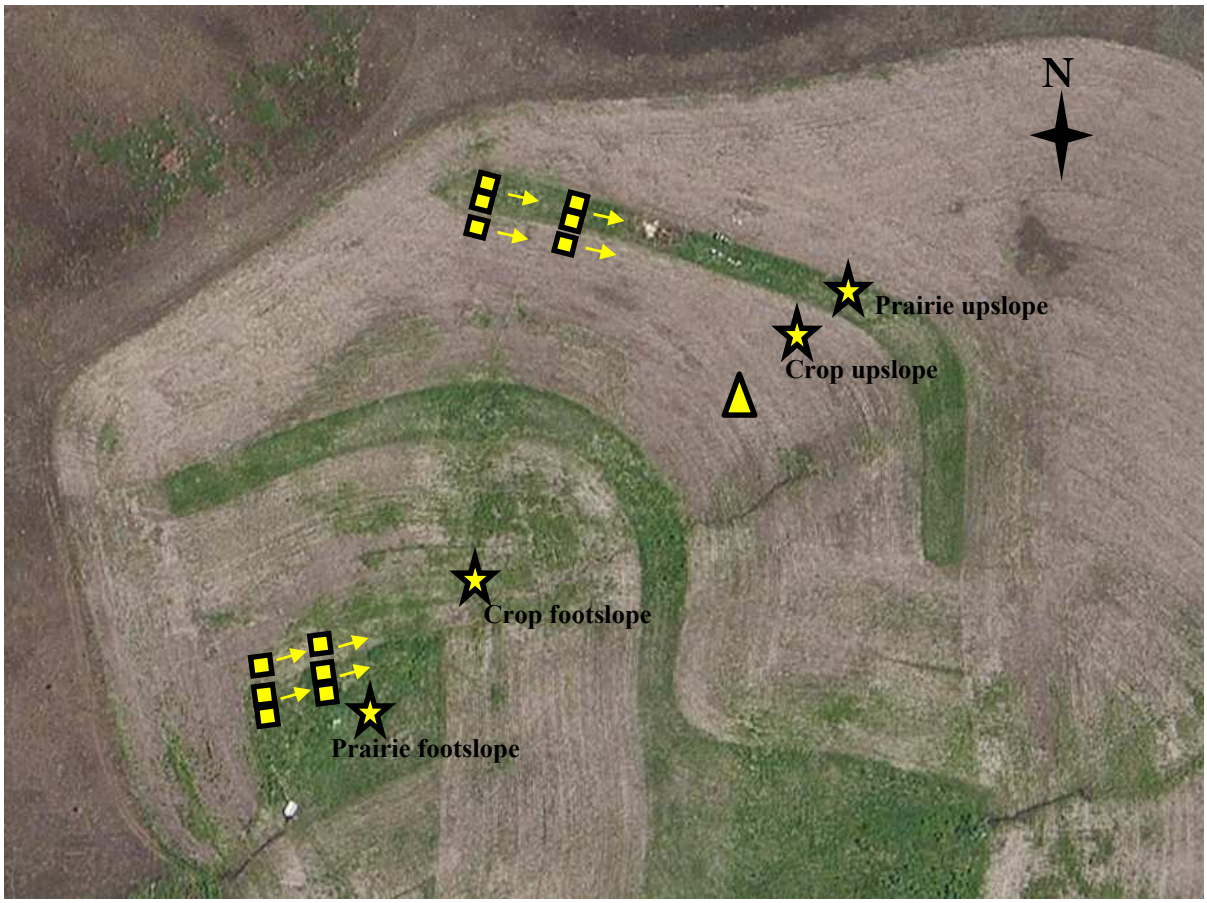


Figure 2. Study sites in a mixed annual-perennial watershed in central Iowa. Stars and triangle show approximate location of micrometeorological stations and Bowen Ratio system, respectively. Squares and arrows represent sap flow plots and direction of plot sampling.

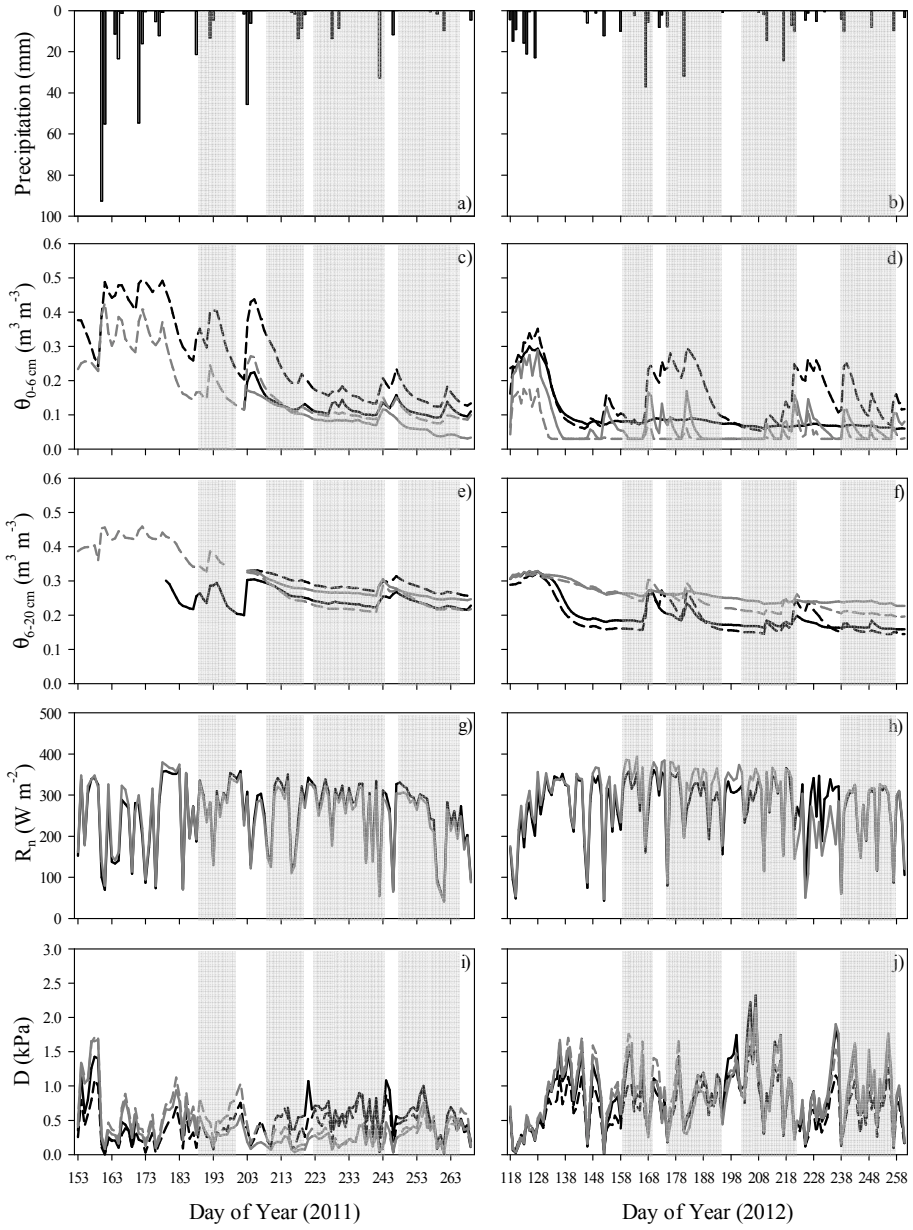


Figure 3. Environmental conditions at the study sites within a mixed-annual perennial watershed in central Iowa in 2011 and 2012: Total daily precipitation (a and b); average daily volumetric soil water content at 0-6 cm ($\theta_{0\text{-}6\ cm}$, c and d); average daily volumetric soil water content at 6-20 cm ($\theta_{6\text{-}20\ cm}$, e and f); average diurnal net radiation (R_n>0, g and h); and average daily vapor pressure deficit (D, i and j). In c-f and i-h, black solid line and black dashed line stand for prairie upslope and prairie footslope, respectively; whereas gray solid line represents crop upslope and gray dashed line corresponds to crop footslope. In g-h, black and gray line stands for prairie and crop site, respectively. Shaded areas show the periods when sap flow measurements were collected.

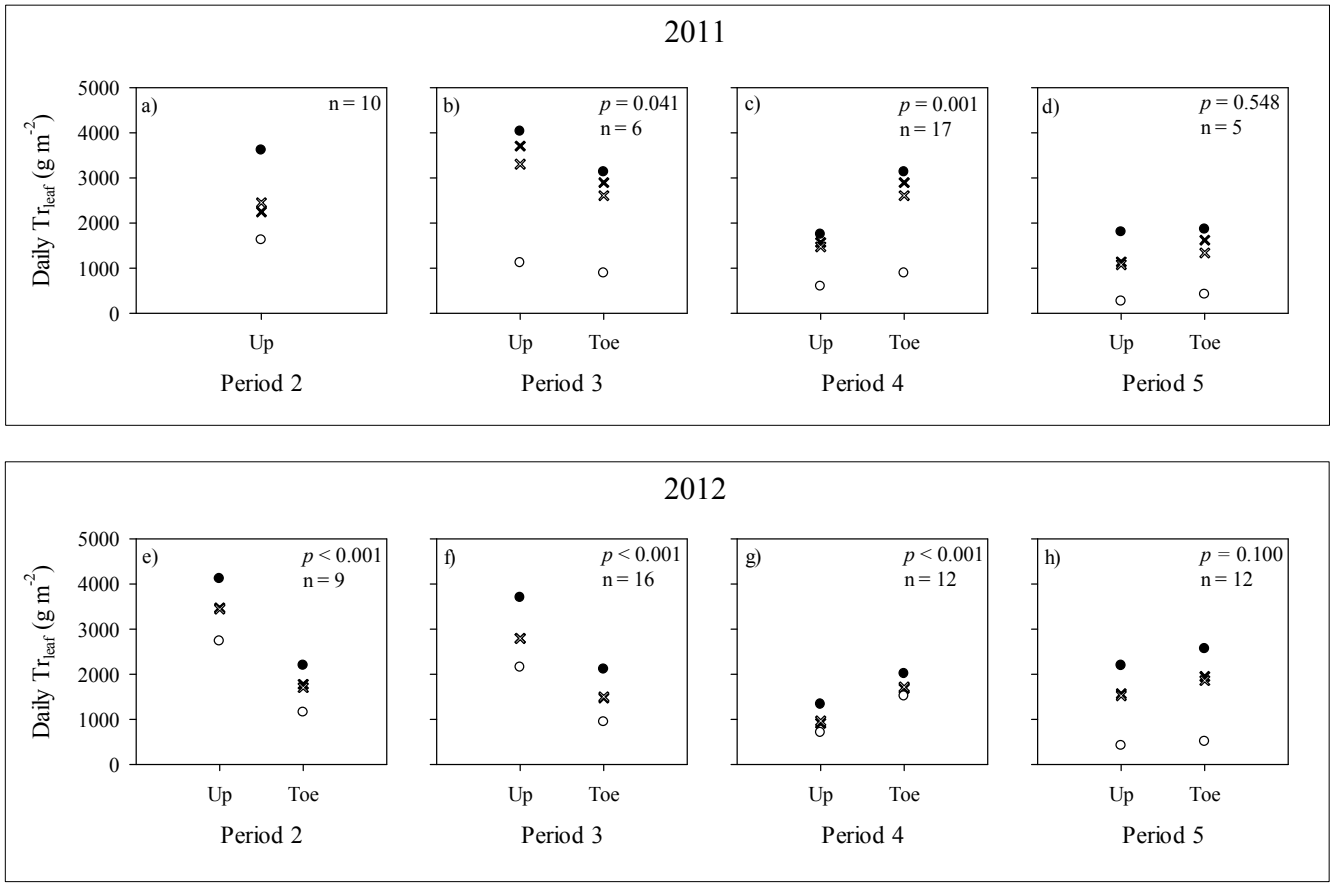


Figure 4. Comparisons of daily transpiration (Tr_{leaf}) by topographic position for *S. canadensis* in 2011 (a-d) and 2012 (e-h). Filled circle, filled cross, empty cross, and empty circle represent the maximum, median, mean, and minimum daily Tr_{leaf} , respectively, for each period; n stands for the number of days used to conduct the paired comparison. There is not data available for footslope position in period 2 in 2011 (a) due to equipment failures. Period 4 in 2011 (c) includes predicted data.

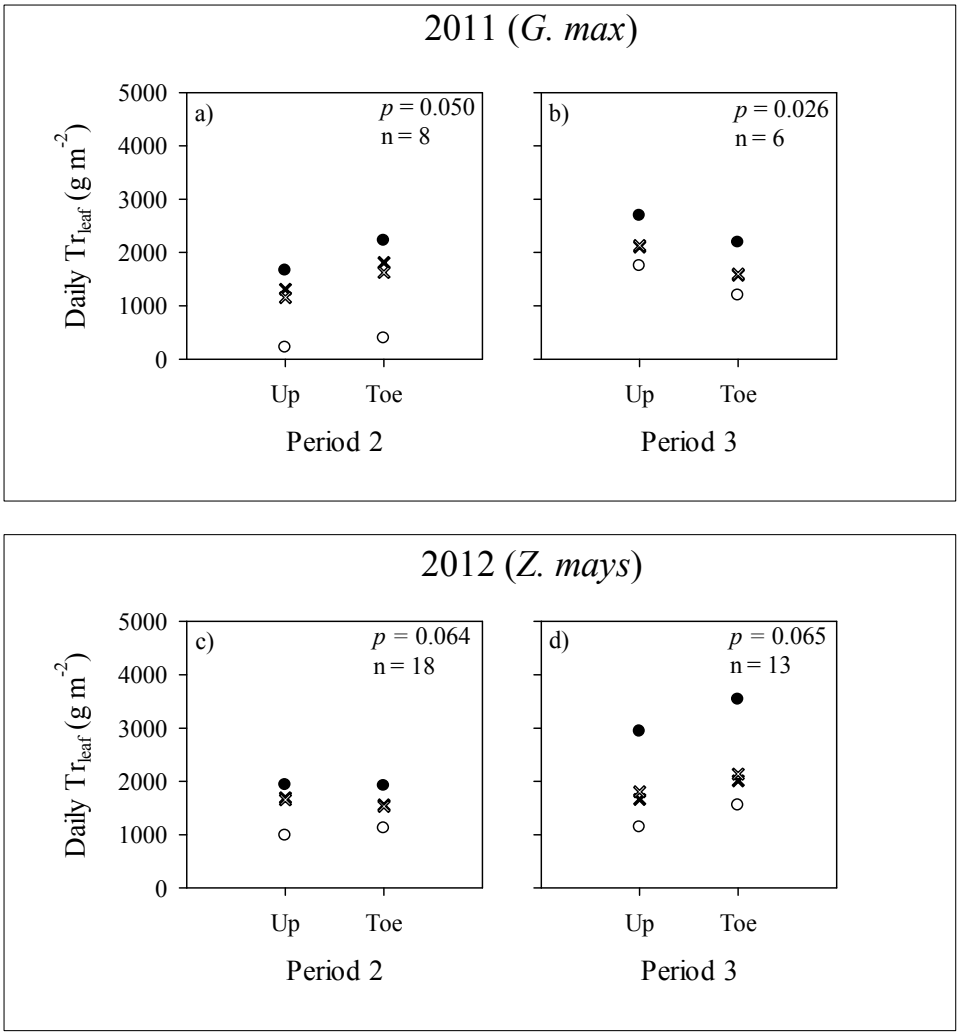


Figure 5. Comparisons of daily transpiration (Tr_{leaf}) by topographic position for *G. max* in 2011 (a-b) and *Z. mays* in 2012 (c-d). Filled circle, filled cross, empty cross, and empty circle represent the maximum, median, mean, and minimum daily Tr_{leaf} , respectively, for each period; n stands for the number of days used to conduct the paired comparison. Period 3 in 2012 (c) includes predicted data.

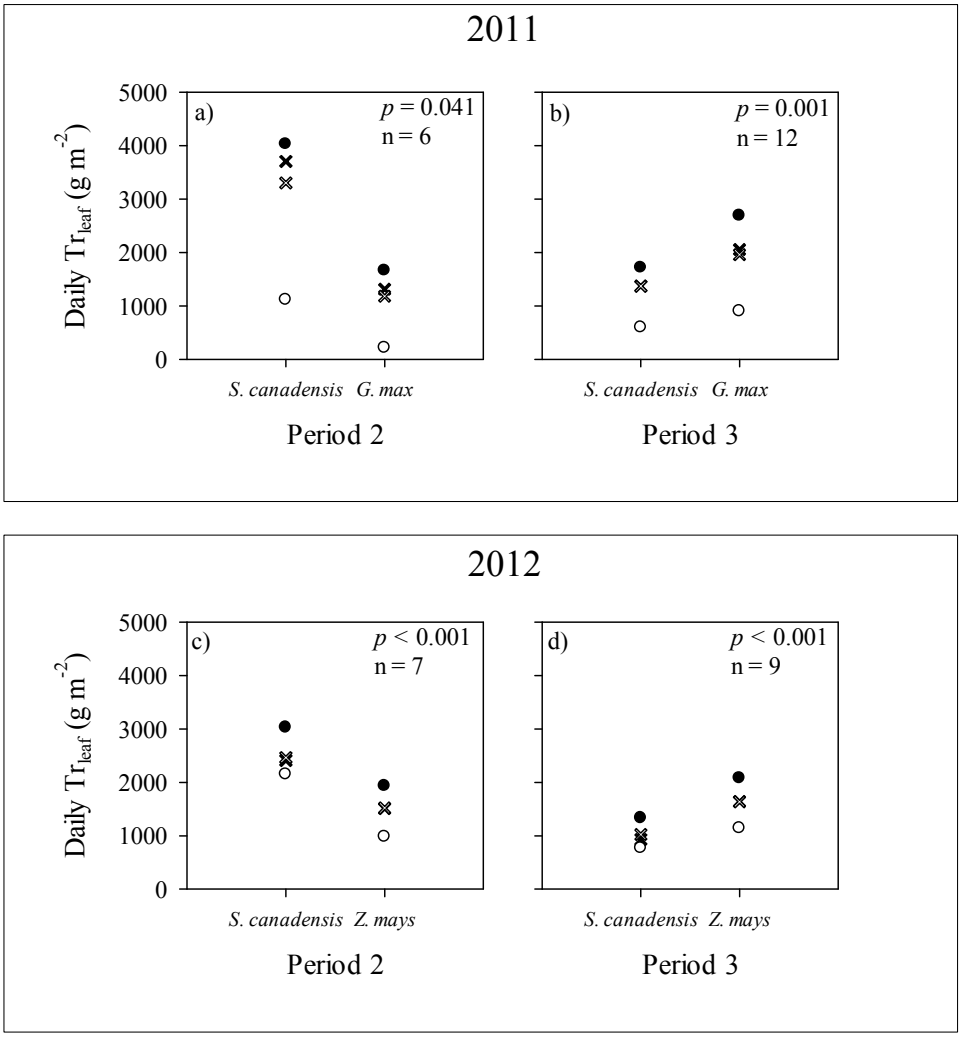


Figure 6. Comparisons of daily transpiration (Tr_{leaf}) for *S.canadensis* and *G. max* (a-b) and *Z. mays* (c-d) at upslope position. Filled circle, filled cross, empty cross, and empty circle represent the maximum, median, mean, and minimum daily Tr_{leaf} , respectively, for each period; n stands for the number of days used to conduct the paired comparison.

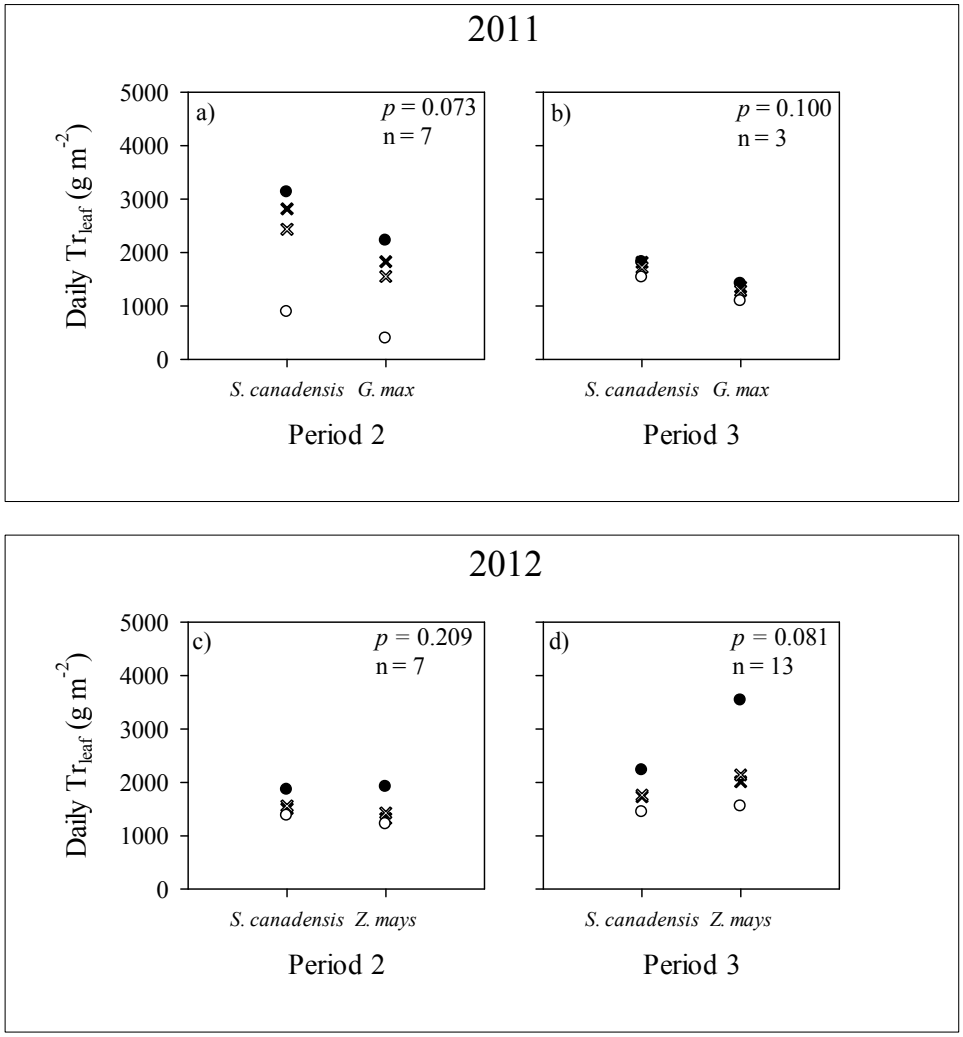


Figure 7. Comparisons of daily transpiration (Tr_{leaf}) for *S.canadensis* and *G. max* (a-b) and *Z. mays* (c-d) at footslope position. Filled circle, filled cross, empty cross, and empty circle represent the maximum, median, mean, and minimum daily Tr_{leaf} , respectively, for each period; n stands for the number of days used to conduct the paired comparison.

CHAPTER 5: TRANSPIRATION RESPONSE TO REWATERING IN PRAIRIE SPECIES AND ANNUAL CROPS AFTER INITIATION OF TWO WATER STRESS LEVELS

A paper to be submitted to *Environmental and Experimental Botany*

Vilma S. Mateos-Remigio, Richard C. Schultz, Jesse A. Randall, Heidi Asbjornsen

Abstract

Because plant transpiration is responsible for returning most of the soil water to the atmosphere, species with high responsiveness to extreme precipitation events may help in the hydrological stabilization of agricultural watersheds. A greenhouse study was conducted to assess the transpiration response to rewatering in two prairie species (*Solidago canadensis* and *Andropogon gerardii*) and two crop species (*Glycine max* and *Zea mays*) after they were exposed to moderate and severe water stress levels (45-35% and 25-15% of field capacity, respectively). The response to soil drying was also examined since it influences the recovery process, and similar behavior was found between *Z. mays* and *S. canadensis*, as they both exhibited a significant reduction in daily transpiration until plants had passed the moderate water stress level. In contrast, transpiration of *G. max* and *A. gerardii* was significantly affected by water shortage before soil water content reached the moderate water stress level, although a more delayed response was observed in *G. max*, suggesting a higher stomatal sensitivity in the prairie grass. A fast and full recovery was observed in the prairie species the same day they were rewatered to field capacity regardless of the stress level experienced. In

contrast, crop response was influenced by the stress intensity, and *G. max* exhibited a more delayed reaction than *Z. mays*. We conclude that prairie species may be more efficient at extracting excess water from a large precipitation event following a dry period compared to annual crops. Future work should focus on evaluating the impacts of differing water use strategies by annual and perennial vegetation at the watershed scale, and the implications for resilience and acclimation to extreme events.

Introduction

In the US, analysis of historical data have shown that precipitation has risen (Karl and Knight, 1998; Pryor et al., 2009) and the largest increase has occurred in the Midwest and Great Plains regions (Barandiaran et al., 2013; Mishra et al., 2010; Steffens and Franz, 2012). In addition, an upward trend in both the frequency and magnitude of extreme precipitation events has also been observed (Todd et al., 2006, Groisman et al., 2012, Villarini et al., 2013). The impact of precipitation variability in the Midwest has likely been intensified as a consequence of the large scale conversion of native perennial vegetation to annual row crops that has taken place in this region. Intensive mechanized agriculture has altered natural soil structure (Brye and Pirani, 2005) increasing soil bulk density and reducing infiltration rates (Radke and Berry, 1993). Agriculture may have also caused an increase in water table as crops are more limited in using deeper groundwater compared to deep rooted native perennial species (Schilling and Jacobson, 2010). Furthermore, soil moisture under crop fields is generally higher than under perennial vegetation (Gutierrez-Lopez et al., 2014; Mateos-Remigio et al., Chapter 2 in this dissertation), thereby reducing soil moisture storage capacity during a precipitation event. Consequently the combined effect of climate change

and agriculture increases the potential for runoff (Tomer and Schilling, 2009; Frans et al., 2013) and nutrient export (Randall and Mulla, 2001; Nangia et al., 2010) in the Midwestern US.

Plant transpiration accounts for 80-90% of terrestrial evapotranspiration (Jasechko et al., 2013). The important role of this process in returning most of the soil water to the atmosphere advocates for the use of plants with high responsiveness to extreme events to mitigate the impact of both climate change and agricultural activities. In the Midwest, incorporation of strips of native perennial vegetation within agricultural watersheds is being promoted as a means of reducing runoff and nutrient loads into streams (Hernandez-Santana et al., 2013; Zhou et al., 2014) that accompany precipitation events. It has been shown that perennial systems have higher infiltration rates (Bharati et al., 2002; Anderson et al., 2009) and soil moisture storage capacity (Gutierrez-Lopez et al., 2014; Le et al., 2011) than the same soils under annual crops, thereby enhancing the downward movement of water. However, much less attention has been given to transpiration patterns of native prairie vegetation in response to water inputs and its potential to accelerate soil moisture loss and improve hydrologic regulation.

Although far from conclusive, studies that have measured the effect of rain or watering on stomatal conductance (g_s) and transpiration of native prairie species and crops provide some evidence that perennial herbaceous species respond more rapidly to changes in soil moisture availability than annual crops. For example, under field conditions, Martin et al. (1991) found that 9 (7 C_3 forbs and 2 C_4 grasses) out of 12 species from a tallgrass prairie in northeastern Kansas exhibited a significant g_s increase as a response to a rain event occurring after a drought period. Also in a field study, Mateos-Remigio et al. (see Chapter 2 in this

dissertation) observed that two prairie species (*Andropogon gerardii*Vitman and *Ratibida pinnata* (Vent.) Barnhart), a C_4 grass and C_3 forb, respectively) increased their transpiration rates following a precipitation event that was preceded by two weeks without rain. In a rain-out shelter experiment, Swemmer et al. (2006) found that *A. gerardii* exhibited a rapid and significant recovery in g_s after rewatering plants that were allowed to wilt.

For crops, specifically for *Zea mays* L. (corn) and *Glycine max* (L.) Merr (soybean), which dominate the Midwest landscape, there is substantial information about the response of transpiration and g_s to dry-down (Ray and Sinclair, 1997; Inamullah and Isoda, 2005; Vitale et al., 2009; Schmidt et al., 2011; Ge et al., 2012; Seversike et al., 2014). However, very few studies, all conducted under greenhouse conditions, have assessed the response to rewatering (Guo et al., 1998). In a study with corn plants that were subjected to different drought levels, Guo et al. (1998) found that transpiration rates recovered within 2-4 days after rehydration. Hura et al. (2006) showed that corn plants fully recovered g_s and transpiration rates within 6 days of daily watering that followed a 14-day drought period. In a soybean experiment, Wang et al. (2006) reported that plants subjected to 4 days without irrigation reached transpiration rates comparable to the control plants two days after rewatering.

If these trends of apparently greater responsiveness in water uptake by prairie species following sharp increases in soil moisture availability compared to crop species represent a consistent pattern associated with inherent differences in their physiologies, this would have implications for using prairie vegetation to mitigate the impacts of heavy precipitation events in agricultural landscape. However, there is currently insufficient comparative data about how annual crops and native prairie species respond to both soil drying and rewetting to

make informed decisions about promoting mixed-annual perennial systems as a conservation practice in Midwestern agricultural landscapes. To address this research gap, we conducted a study to assess the response to rewatering in two native prairie species (*Solidago canadensis* L.*,* a C_3 forb, and *A. gerardii*, a C_4 grass) and two crops (*G. max,* C_3, *and Z. mays,* C4) after being subjected to two different water stress levels. Based on previous findings discussed above, we hypothesized that prairie species would show a more rapid and pronounced response to rewatering than corn or soybean plants. Because controlling water inputs is challenging under field conditions, the study was conducted under greenhouse conditions.

As this study is part of a bigger project that seeks to evaluate the ecohydrological impact of incorporating strips of native perennial species into experimental watersheds under corn-soybean rotations, the selections of species was based on the species growing in the field. *Solidago canadesis* is the most dominant species in the strips throughout the whole growing season, and *A. gerardii* becomes visible, but not dominant, in the second half of the growing season when conditions are warmer. Since it is known that C_3 and C_4 groups differ in their water requirements, the inclusion of *A. gerardii* in the greenhouse experiment allowed us to have a representative species from the two photosynthetic groups that are growing in the experimental watersheds.

Materials and Methods

Plant cultivation and greenhouse conditions

The study was conducted in the Forestry greenhouse at Iowa State University. Prairie species seeds were purchased from Ion Exchange, Inc. (Harpers Ferry, IA) and subjected to cold (*A. gerardii*) and cold-moist (*S. canadensis*) stratification treatment for 30 days (W.

Johnson, Iowa DNR Prairie Resource Center, pers. comm.) Initially, both prairie species seeds were sown in plug trays (60 x 35 x 15 cm); however, the germination rate of *A. gerardii* was low. Therefore, two weeks after the first attempt, additional *A. gerardii* seeds were sown in flats (54 x 27 x 6 cm) where germination rate substantially improved. Crop species seeds were also germinated in flats. Seedlings were maintained in the plug trays and flats until transplanting into plots. A growing media (Metro-mix 300, Sun Gro Horticulture, Canada CM Ltd.) was used as a substrate for germination of all the seeds. Prairie species were sown four months earlier than crops because of the faster growth rates of crops (Table 1).

At 149 and 8 days after sowing prairie and crop seeds, respectively, 125 seedlings per species were transplanted to individual pots (Hummert International, Earth City, MO) of two sizes: ~ 3.8 L for prairie species and 7.6 L for crops. Pots were previously filled with a substrate (hereafter referred to as soil) that consisted of 75% washed sand (Hallet Materials, Ankeny, IA) and 25% of the same growing media used for germination. Pots were watered daily, weeded regularly to remove undesirable plants, and fertilized twice per week (except for *G. max* that was fertilized only once per week) with a 3:1 mix of Cal-Mag 15-5-15 plus micronutrients fertilizer and an all-purpose 21-5-20 plus micronutrients (Peters Excel, Everris NA, Inc.). The experiment was conducted under natural light conditions and the greenhouse temperature was set at 21°C in the day and 19°C at night.

Field capacity estimation

Field capacity (FC) for the soil used in the experiment was estimated gravimetrically before initiating the experimental treatments. Four pots without plants were saturated until

they dripped and allowed to drain over 12 hours at night. Pots were weighed the next morning under the assumption that the soil was at FC. The soil was then oven-dried at 105 °C for 24 hours and the dry weight was recorded to calculate gravimetric water content (0.17 g g^{-1}) and bulk density (1.2 g cm^{-3}). The volumetric water content (θ) at FC was 0.20 m^3 m^{-3}.

Experimental design and treatments

A total of 81 plants per species were selected for measurements from a population of 125 plants and each species was placed on a different bench within the greenhouse bay. In each species, the experiment was repeated three times at different plant ages (hereafter referred to as "age 1", "age 2" and "age 3", Table 1) in *G. max*, *A. gerardii* and *S. canadensis*, whereas only one experiment was conducted in *Z. mays* because plants were close to physiological maturity when the first measurement began.

Henceforth, the methodology is described for a single species, but it was applied to all species unless otherwise stated. Age 1experiment was started by randomly selecting 27 pots and assigning each to one of the following three treatments (27 pots ÷ 3 treatments = 9 pots/treatment):

1) FC or "well-watered": pots were watered every day to maintain FC. This was used as the control group.
2) 45-35FC or "moderate water stress": watering was withheld until soil water content reached between 45% and 35% of FC.
3) 25-15FC or "severe water stress": watering was withheld until soil water content reached between 25% and 15% of FC.

The 54 remaining pots were maintained with daily watering until the next repetition was started, and then another 27 were randomly selected following the same protocol. Finally, the last 27 pots were used for age 3 experiment. In cases where plants were injured or broken, the total number of plants was reduced, resulting in somewhere between six to nine plants per treatment. Three extra pots containing only soil (without plants) were incorporated into each treatment to estimate evaporation. These pots were randomly placed between the pots containing plants.

Daily transpiration measurements

Measurements began once species reached the flowering stage, and because species have different growth rates, experiments were begun at different times starting with *G. max*, followed by *Z. mays*, then *A. gerardii* and lastly *S. canadensis*. Experiments were initiated by saturating the pots (with plants and without plants) at evening. Pots were weighed the next morning assuming again that they were at FC. Pots were weighed every subsequent morning starting at 6:00 h (local standard time) to estimate the amount of water lost during the previous day. Weighing was finished by 7:30-8:00 h, when R_s was still <100 W m^{-2} (data not shown). Although some water loss may have occurred during that period, transpiration rates are generally small when available energy is less than 200 W m^{-2} (Sauer et al., 2007); therefore, we assumed that the transpiration was negligible and did not affect our daily transpiration measurements.

The first day of water loss estimation was defined as day 0. Pots in the FC treatment were rewatered every day with the same amount of water as had been lost the previous day in order to maintain them at FC. Pots under the water stress treatments were rewatered to FC

the morning they reached moderate (45-35% of FC) and severe water stress levels (25-15% of FC), respectively. Water loss was estimated from the day when pots were rewatered and the following day. Average daily evaporation from pots without plants in each treatment was subtracted from the daily water lost from pots with plants to estimate daily net plant transpiration (T_d) [g day^{-1}].

Water potential measurements

In order to estimate the actual stress experienced by plants once they reached a determined water stress level, predawn water potential (Ψ) [MPa] was measured in leaves of 3-5 plants randomly selected from the 6-9 pots per treatment. Plants were visually divided into four sections, and two healthy leaves located in the third segment (from the top to the bottom, Fig. 1) were removed with a sharp cutter. Samples were immediately placed in plastic bags to avoid dehydration (Turner and Knapp, 1996). Each leaf was then placed in a Scholander chamber (PMS Instrument Company, Albany, OR) and the pressure at which water was observed (end point) on the cut surface was recorded. A 10x magnifying glass was used to recognize the end point. The Ψ for each treatment was then estimated as an average of 6-10 measurements.

Stomatal conductance and light measurements

To support our T_d data, we also conducted simultaneous measurements of g_s [mmol m^{-2} s^{-1}] and photosynthetically active radiation (PAR) [µmol m^{-2} s^{-1}] during the dry-down period in Z. *mays*, *A. gerardii* and *S. canadensis*. Generally, the response of g_s to PAR is expressed by a hyperbolic relationship (Turner, 1991):

$$g_s = \frac{a*PAR}{b+PAR} \quad (2)$$

where *a* and *b* are parameters that represent maximum g_s and slope of the response, respectively (Kim and Verma, 1991). In this study we were interested in *a*, as it was expected to reflect the effect of changing soil water conditions on plant water use. A porometer (SC-1 Leaf porometer, Decagon Devices, Pullmand, WA) was used to measure g_s, while PAR was measured with a quantum sensor (LI-190, LI-COR Inc., Lincoln, NE). Data were collected every two hours from 9 am to 7 pm on 2-3 top leaves from three pots randomly selected from the 6-9 in each treatment. When humidity was above 75% we were unable to calibrate the porometer and measurements were therefore not taken.

Environmental conditions

Hourly solar radiation (R_s) [W m^{-2}] data were obtained from the Iowa Environmental Mesonet, Ames station, located approximately 10 km east of the greenhouse. Hourly values were averaged over a 24-hour period to obtain daily average R_s. We also calculated the diurnal average of R_s for the days when T_d was measured to verify that although the experiments in each species were conducted at different time (starting on June 25 with *G. max* and ending on September 13 with *S. canadensis*), the light conditions were similar throughout the whole measurement period (See Appendix A).

Vapor pressure deficit (*D*) [kPa] was estimated from data recorded every minute with temperature/relative humidity sensors (HOBO U10 Data Logger, Onset Computer Corporation, Cape Cod, MA) that were placed on the benches. First, saturated vapor pressure (e_s) was calculated as follows:

$$e_s = a\ exp\left(\frac{b\ T}{T+c}\right) \quad (3)$$

Where a, b and c are constants (0.611, 17.502 and 240.97 respectively) and T is air temperature recorded with the sensor. Second, actual vapor pressure (e_a) was calculated with the following equation:

$$e_a = \frac{RH}{100}\, e_s \quad (4)$$

Where RH is relative humidity. Finally, vapor pressure deficit was derived by subtracting e_a from e_s and the resulting values were also averaged on a daily basis.

Data organization, analysis and estimation of parameters

The Shapiro-Wilk test was used to check for normality, and we found that no data transformations were needed. Preliminary analysis of variance (ANOVA) of main effects (treatment and age) and their interaction showed that there was no significant effect of interaction ($P > 0.05$) in all species, while treatment and age had a significant effect on T_d of *G. max* ($P = 0.038$ and $P = 0.002$, respectively) and *A. gerardii* ($P = 0.003$ and $P < 0.001$, respectively). *Solidago canadensis*' T_d was not influenced by age ($P = 0.670$), whereas no treatment effect was observed in *Z. mays* ($P = 0.084$). The ANOVA was run again dropping the interaction term to redistribute the error in the main effects (Bancroft, 1964, Table 2). Based on these results, experiment repetitions were analyzed separately. Given that experiments were conducted at different times in all species, we chose a conservative approach and did not make statistical comparisons among species.

Daily significant differences among treated plants relative to their control group were calculated with the Tukey-Kramer test using the Glimmix procedure of SAS (SAS Institute, Inc. Cary, NC, USA). For a better visualization of the T_d response to soil dry-down and rewatering, we calculated the transpiration ratio by dividing the daily transpiration for each

stressed plant by the average daily transpiration from the plants in the control group. This normalization also eliminated the effect of daily environmental variations (Ray and Sinclair, 1997).

Significant differences in Ψ among treatments were estimated with one-way ANOVA and post-hoc pairwise multiple comparisons were conducted with the Tukey test. We pooled g_s/PAR data together across all the days to estimate a single or global a parameter for the water stress period in each species. The parameters in the hyperbolic curve were estimated by fitting g_s to PAR using non-linear least square regression (Kim and Verma, 1991).

Results

Results are presented separately by species. Daily transpiration was plotted along with daily R_s and D to show that variation in T_d (mainly from the control groups) usually followed changes in both variables. Average leaf area of the plants for each experiment is presented in Table 1.

Glycine max

As expected, maximum T_d across each experiment always occurred in plants maintained at FC, except at age 3 when this species did not show any response to water stress (Fig. 2d-f). Moderate water stress was attained on the morning of days 5, 4 and 3 at age 1, 2 and 3, respectively, whereas severe water stress was reached one or two days later. Plant water potential (Fig. 2g-i) under well watered conditions was fairly consistent in all experiments, and decreased significantly with water stress at age 1 and 2 ($P < 0.001$). At age 2, plants subjected to severe water stress were in the lower range of water stress experienced

by this species (20% of FC). At age 3, moderate water stress did not have any effect on Ψ, but it significantly dropped when plants were at severe water stress ($P < 0.001$).

Transpiration ratio presented in Fig. 3a shows that T_d was not reduced in the water stress treatments within the first two days of withholding water. Then, T_d abruptly dropped when plants were close to moderate water stress and it continued declining as soil water content was approaching severe stress. Age 3 experiment was not included since no response was observed. Plants subjected to both levels of water stress were able to respond to rewatering one day after they were irrigated to FC, except those plants subjected to severe water stress at age 2 (Fig. 3b).

Zea mays

In *Z. mays* plants, the experiment was conducted over a period of 6 days. Moderate and severe water stress levels were reached on day 3 and 4, respectively (Fig. 4b). Even though Ψ was doubled at moderate stress, a significant effect ($P < 0.05$) was observed only at the severe water stress level when Ψ was approximately 3 times lower than in plants from the control group (Fig. 4c).

As in the *G. max* experiment, there was no immediate significant reduction in T_d due to water stress. However, from Fig. 5a it is clear that T_d in stressed plants showed a downward trend following day 1 of withholding water. A significant difference was observed until day 3 ($P = 0.0049$), when plants were close to the severe water stress stage. This result is supported by the *gs*/PAR curve (Fig. 6), although maximum g_s was similar among treatments when all days were pooled together. The response to rewatering varied among treatments (Fig. 5b). Plants subjected to moderate water stress showed a full recovery the

same day they were rewatered. However, plants that experienced severe stress responded to rewatering one day later and did not show full recovery.

Andropogon gerardii

Plants reached moderate stress on the morning of day 6 (age 1), 5 (age 2) and 3 (age 3), respectively (Fig. 7d-f). Plants reached the severe water stress level one day later at age 1 and 2, and two days later at age 3. In all experiments, moderate stress did not affect plant water status, as Ψ was similar to that in plants at FC, whereas a significant reduction ($P < 0.05$) was observed when plants were at the severe water stress level (Fig. 7g-i).

Daily response to soil dry-down displayed slight variations with age of plants; nonetheless, T_d was significantly affected ($P < 0.05$) by water stress imposition on some days even before plants experienced moderate stress in all experiments (Fig. 8a). The steepest decline in T_d occurred on the first day after water was withheld and thereafter more moderate changes were observed. The effect of water stress on g_s somewhat resembled the effect on T_d as is shown by the *gs*/PAR curves generated for age 1 experiment (Fig 9). On the other hand, the response to rewatering was consistent among all experiments, and water-stressed plants exhibited immediate recovery regardless of the experienced water stress level (Fig. 8b).

Solidago canadensis

Unlike the other species, age did not have a significant effect on *S. canadensis* experiment, yet results are presented separately (Fig 10d-f). Moderate and severe water stress levels were attained on the same day for all experiments (day 2 and 3, respectively). Severe

water stress caused a significant reduction in Ψ in all experiments ($P < 0.05$), while moderate water stress had a significant effect ($P < 0.05$) on Ψ only at age 2 (Fig. 10g-i).

The drying response pattern was similar to that found in *A. gerardii*, but a significant reduction in T_d was observed when plants were beyond moderate water stress and close to severe water stress levels ($P < 0.05$, Fig. 11a). This result did not agree with g_s measurements for the same day, although global maximum g_s did decline in plants under water stress treatments (Fig. 12).The response to rewatering in this forb species is also comparable to the one observed in the grass. Plants subjected to both water stress levels showed rapid recovery following rewatering, except for plants subjected to severe water stress at age 2 (Fig. 11b).

Discussion

Our study aimed to evaluate the transpiration response to soil dry-down and rewatering in two crops and two prairie species under greenhouse conditions. Given that prairie plants are smaller than crops, a larger pot size was used to grow the crop plants. We assumed the pot size effect was insignificant because roots in all species were well distributed throughout the pots (see Appendix B).

Validation of *Td*

Daily transpiration values for the species measured in this study are comparable to those reported in other studies that used the same method of estimation in greenhouse experiments. For example, average T_d (200 g day^{-1} plant^{-1}) in *G. max* plants under FC treatment (age 1) was only ~50 g higher than the average found by Serraj et al. (1999) for well watered plants over a period of 17 days. The difference might be partially explained by

age of the plants, which were approximately 20 days older in our study. For *Z. mays*, average T_d (277 g day^{-1} plant^{-1}) in plants from the control group was approximately 48 g lower than that reported by Ray and Sinclair (1998) for plants maintained under a similar irrigation regime, but growing in containers 1.5 l larger; and higher by 30 g than plants growing in containers that were smaller by approximately 3.4 L.

No studies showing daily transpiration in *A. gerardii* under greenhouse conditions were found. However, Senock and Ham (1995) reported T_d that was estimated gravimetrically in *A. gerardii* plants growing in pots and maintained in the field under well watered conditions. Measurements taken in June and July ranged from 46 to 93 g day^{-1} plant^{-1}. These values are similar to those found in this study (34-80 g day^{-1} plant^{-1}) for plants under FC treatment throughout the 3 repetitions conducted. We did not find published information for *S. canadensis* transpiration; however, values observed in this study for plants without water stress (100-200 g day^{-1} plant^{-1}) are comparable to daily measurements collected in the field by Mateos-Remigio et al. (unpublished data) using the sap flow technique, who found maximum daily transpiration was 140 g day^{-1} plant^{-1}.

Response to soil dry-down

Most published work has usually evaluated transpiration or g_s response to water stress on the basis of the fraction of available soil water, as the main objective has been to determine the critical point at which plants begin to close their stomata. In this study, we primarily wanted to determine whether species were able to respond to rewatering and how complete the response was, hence the response to both soil dry-down and rewatering was

assessed on a daily basis by comparing T_d in water-stressed plants against T_d in well-watered plants.

The insensitivity of *G. max*'s water use to the first days of soil drying observed in our study is consistent with previous reports. Liu et al. (2003) showed that g_s in soybean plants under water stress was similar to that of well-watered plants during the first 8 days of induced water stress, followed by significant declines. The difference in number of days with respect to this study may be due to the age and size of plants, which were half the age of our plants. Thus, water depletion in their study was slower. Using plants of similar age as ours, Wang et al. (2006) found that both transpiration rate and g_s in plants subjected to water withholding dropped below that of control plants starting on day 3 of treatment period. The response pattern to water stress in *G. max* could be explained by chemical and hydraulic processes occurring in the plant. It is recognized that the hormone abscisic acid (ABA) plays a major role in regulating g_s closure under water stress (Davies and Zhang, 1991; Tardieu and Davies, 1992; Christmann et al., 2007). In addition, it has been suggested that changes in xylem sap pH also participate in chemical signaling during soil drying (Schachtman and Goodger, 2008). In the study conducted by Liu et al. (2003) it was found that the concentration of xylem and leaf ABA and xylem sap pH remained similar among water-stressed and well-watered plants until 9 and 14 days after stress onset, respectively. This delay in signaling might explain the lack of sensitivity to early stages of stress in our study, where Ψ increased significantly even at moderate stress levels, and it in turn possibly caused the sudden decline in T_d.

In the experiment with *Z. mays*, T_d in water-stressed plants gradually diverged from the control group after day 1. This pattern might be due to a rapid increase in ABA content

and a change in xylem pH as has been shown in some studies (e.g. Bahrun et al., 2002; Wang et al., 2008; Pirasteh-Anosheh et al., 2013). Although significant difference were found only when plants had passed the moderate stress level (day 3), our T_d and Ψ results advocate for a chemical control in the early water stress period. Surprisingly, the global maximum g_s represented by *a*, was not reduced as a consequence of water stress, on the contrary, it showed a slight increase. Clear reduction in g_s was observed on day 3 (analogous to T_d); nonetheless, because g_s in plants from the water stress treatment was higher than in plants from the control group on day 1, no differences were observed in the overall parameter *a*. This increase in g_s is not unusual. Vitkauskaite and Venskaityte (2011) reported that g_s in barley (*Hordeum vulgare* L.) increased significantly when exposed to moderate water stress.

Daily transpiration in both *A. gerardii* and *S. canadensis* plants experiencing water restriction deviated from control groups following day 1 of treatment, but the species differed in the water stress level at which a significant effect was found. In *A. gerardii*, significant differences were observed even before plants reached the moderate stress level without any change in Ψ. It suggests a tight stomatal regulation on transpiration and control of plant water status in the early stage of soil drying. Measurements of g_s at age 1 somewhat reflected the same pattern found in T_d measurements. As expected, maximum g_s was lower in the water stress treatment than in the control group. The difference was more evident until the water-stressed plants were close to the severe stress level. We are not aware of studies assessing the effect of water stress on daily transpiration in *A. gerardii*, but Awada et al. (2002) evaluated g_s response to water withholding in four C_4 grasses from the Nebraska Sandhills and they found g_s sharply declined in the first 4 days of soil drying. Despite a lack of published data about chemical changes occurring in prairie species as a function of water stress, the rapid

response to soil water deficit found in our study may be due to an immediate chemical response and signaling from roots to shoots, as occurs in *Z. mays*.

Solidago canadensis had the shortest drying period among all species due to the high water use rates, which caused faster water depletion compared to *A. gerardii*. Consequently, moderate water stress was reached one day after water was withheld well before any significant reduction in T_d occurred. Overall, the response in T_d and Ψ to soil drying was comparable with our findings in *Z. mays,* although the T_d decline was steeper in *S. canadensis*. Contrary to observations in *Z. mays*, global maximum g_s in stressed plants indicated a slight reduction relative to the plants under non-water limitation, even though maximum g_s on day 3 was higher for the former. Ripley et al. (2010) found that g_s in C_3 grasses decreased more than in C_4 grasses over a 36-day drought period. Based on leaf water potential values that were less negative in C_4 than in C_3, they attributed g_s results to higher hydraulic conductance in the C_4 grasses. In our experiment, Ψ at moderate water stress was also less negative in the C_4 grass than in the C_3 forb. At the severe water stress stage, Ψ was comparable among both species. Similar results were found in Ripley's (2010) experiment when measurements were taken 49 days after stress onset.

In *G. max* and *A. gerardii*, moderate and severe water stress levels were reached at different number of days every time the experiment was repeated. We attribute this result to differences among in leaf area and daily average R_s. For example, in *G. max* experiment the average leaf area (Table 1) and average daily R_s during the first three days of treatment was larger at age 2 than at age 1 (Fig. 2d-e), which resulted in higher transpiration rates at age 2 experiment. In the *A. gerardii* experiment there were no trends in average leaf area, but

average daily R_s during the first three days was also higher every time the experiment was repeated (Fig. 7d-f).

Response to rewatering

While response to water stress has been relatively well studied in numerous species, little is known about the capacity of recovery and even less about the mechanisms involved in the recovery process following water stress (Galle et al., 2007). In this study we wanted to determine the rate of rehydration response immediately after rewatering. Based on previous literature, we expected a higher water use in prairie species after rainfall that is preceded by a dry period. Full and rapid response was defined as the absence of a significant difference in T_d from treated plants relative to the control group since the day of rewatering.

Response to rewatering is strongly dependent on the stress level experienced by the plant (Galle et al., 2007; Xu et al., 2010). Miyashita et al. (2005) found a complete recovery in g_s, transpiration and photosynthesis in kidney bean (*Phaseolus vulgaris* L.) plants that experienced 2-3 days of withholding water, and the level of recovery decreased as the water restriction period increased. However, even in plants that showed full recovery, g_s and transpiration rates were similar to that of the control group only 5 days after rewatering began. Wang et al. (2006) found that full g_s and transpiration recovery in soybean plants occurred 1 day after rewatering, as in our study. In addition, we also found this pattern was almost consistent regardless of the magnitude of stress. Although we did not find specific information for *G. max*, a delayed response to rewatering observed in other species has been attributed to a subsequent effect of residual ABA that is released from the roots even when plants have been rehydrated (Dorffling et al., 1980; Lovisolo et al., 2008).

Both crops confirmed that the degree of recovery is determined by stress intensity. *Glicine max* plants exposed to severe water stress at age 2 experienced the lower limit of stress. Hence, our results show that the capacity of response to rewatering in *G. max* will likely be restricted when Ψ drops to a value between -0.7 to -1.6 MPa. The response of *Z. mays* in this experiment indicates that this species might be able to respond immediately to water input, but it also depends on the stress level preceding rewatering. In this study, severe water stress (Ψ ~ -1.6 MPa) constrained plants from a rapid reaction to rehydration. Hura et al. (2006) showed transpiration and g_s rates in plants recovering from 14 days of water stress equaled rates in plants maintained without water stress after 6 days of daily irrigation.

As hypothesized, both prairie species exhibited quick and practically full recovery in transpiration (77% to 100% with respect to control groups) the same day their soil water again reached FC regardless of the previous water stress level applied, with the exception of *S. canadensis* plants subjected to severe stress at age 1. As in *G. max*, this lack of response might be explained by the severity of water stress experienced (15% of FC), that dropped plant water potential to -0.8 MPa, which seems to be the threshold at which *S. canadensis* fails to respond rapidly. On the contrary, *A. gerardii* was still able to respond at a similar Ψ, probably due to its intrinsic higher drought resistance. It is likely that *A. gerardii*'s response would have become constrained if subjected to more severe stress. Swemmer et al. (2006) found that g_s rate in *A. gerardi* plants subjected to 15 days of withholding water showed full recovery 2-3 days after rewatering.

In general, our study indicates that the response to rewatering depends on the level of stress reached prior to rewatering and the individual species evolutionary mechanism to deal with drought conditions. As hypothesized, native prairie species exhibited a higher efficiency

in terms of their ability to respond to water input after exposure to two different water stress levels compared with common agronomic crops. The faster response to rewatering observed in prairie species suggests that under field conditions they would likewise respond quickly to a major precipitation event that occurred after prolonged water limitation. A rapid increase in transpiration under such a situation could result in prolonged infiltration of water into the soil as transpiration rapidly removed water creating opportunities for more stored water. This rapid response could reduce the amount of surface runoff that might occur if the recharged soil profile could no longer accept more water because of near saturated conditions.

Conclusions

In this greenhouse study, we measured the T_d response to soil drying and rewatering in two crops typically found in the Midwest agricultural landscape and two native prairie species that grow in the strips planted in watersheds dominated by crops. The main goal was to assess the transpiration response to water inputs that were preceded by two different water stress intensities. Experiments in *G. max* and prairie species started when plants were entering the flowering stage, whereas in *Z. mays*, plants had initiated silking. These stages were chosen because, based on field observations, they occur during the peak of the growing season when all species are at maximum activity. Given that measurements were not taken concurrently in all species, this approach also allowed us to make a reasonable, although not statistical, comparison among species.

Transpiration, g_s and Ψ measurements showed that the studied plant species differed in the way they respond to soil drying, although some similarities were observed between *G. max* and *A. gerardii*, and between *Z. mays* and *S. canadensis*. In *G. max* and *A. gerardii*, T_d

began to drop significantly before soil water content was at moderate stress. However, their response patterns differed. While *A. gerardii's* T_d declined sharply in the first day of withholding water, *G. max* exhibited a delayed response. For *Z. mays* and *S. canadensis*, significant reduction in T_d was observed when plants were between the moderate and severe water stress level. Moreover, T_d from water-stressed plants deviated from the control group immediately following day 1 of water withholding, but a more gradual decline was observed in *Z. mays*.

Response to rewatering was distinct between native perennials and annual crops. Prairie species were found to recover faster than traditional row crops across the induced stress treatment levels. In contrast, both tested crops were more limited, particularly *G. max* which was not able to respond immediately to rehydration regardless of the water stress intensity experienced. These results suggest that native perennial species may contribute to attenuation of runoff not only by improving soil water infiltration as has been shown in several studies, but also by removing more water from the soil when a heavy precipitation event occurs.

We are aware our findings must be validated under field conditions and scaled up to the stand level in order to assess the real impact of perennial strips. Nonetheless, results from this study already represent an important contribution to enhancing our knowledge concerning the multiple benefits of perennial species growing with annual crops. Future work should also include biochemical analysis in order to gain a more complete understanding of all the processes involved in the response to drying and rewatering.

Acknowledgements

Funds for this research were provided by the Leopold Center for Sustainable Agriculture, and the U.S. Department of Agriculture's Agriculture and Food Research Initiative. We thank Christopher Witte, Omar de Kok-Mercado, Brian Noonan, and Leigh A. Long for all their help in the setup of the experiment and data collection.

References

Anderson, S.H., Udawatta, R.P., Seobi, T.,Garrett, H.E., 2009. Soil water content and infiltration in agroforestry buffer strips. Agrofor. Syst. 75(1), 5-16.

Awada, T., Moser, L.E., Schacht, W.H.,Reece, P.E., 2002. Stomatal variability of native warm-season grasses from the Nebraska Sandhills. Can. J. Plant Sci. 82(2), 349-355.

Bahrun, A., Jensen, C.R., Asch, F.,Mogensen, V.O., 2002. Drought-induced changes in xylem pH, ionic composition, and ABA concentration act as early signals in field-grown maize (*Zea mays* L.). J. Exp. Bot. 53(367), 251-263.

Bancroft, T.A., 1964. Analysis + inference for incompletely specified models involving use of preliminary test(S) of significance. Biometrics. 20(3), 427-442.

Barandiaran, D., Wang, S.Y.,Hilburn, K., 2013. Observed trends in the Great Plains low-level jet and associated precipitation changes in relation to recent droughts. Geophys. Res. Lett. 40(23), 6247-6251.

Bharati, L., Lee, K.H., Isenhart, T.M.,Schultz, R.C., 2002. Soil-water infiltration under crops, pasture, and established riparian buffer in Midwestern USA. Agrofor. Syst. 56(3), 249-257.

Brye, K.R.,Pirani, A.L., 2005. Native soil quality and the effects of tillage in the grand prairie region of eastern Arkansas. American Midland Naturalist. 154(1), 28-41.

Christmann, A., Weiler, E.W., Steudle, E.,Grill, E., 2007. A hydraulic signal in root-to-shoot signalling of water shortage. Plant J. 52(1), 167-174.

Davies, W.J.,Zhang, J.H., 1991. Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 55-76.

Dorffling, K., Tietz, D., Streich, J.,Ludewig, M., 1980. Studies on the role of abscisic acid in stomatal movements. In: F. Skoog (Editor), Plant growth substances 1979, Proceedings of the 10th International Conference on Plant Growth Substances. Springer-Verlag, Madison, WI, USA, pp. 274-285.

Frans, C., Istanbulluoglu, E., Mishra, V., Munoz-Arriola, F.,Lettenmaier, D.P., 2013. Are climatic or land cover changes the dominant cause of runoff trends in the Upper Mississippi River Basin? Geophys. Res. Lett. 40(6), 1104-1110.

Galle, A., Haldimann, P.,Feller, U., 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. New. Phytol. 174(4), 799-810.

Ge, T.D., Sui, F.G., Bai, L.P., Tong, C.L.,Sun, N.B., 2012. Effects of water stress on growth, biomass partitioning, and water-use efficiency in summer maize (*Zea mays* L.) throughout the growth cycle. Acta Physiol. Plant. 34(3), 1043-1053.

Groisman, P.Y., Knight, R.W.,Karl, T.R., 2012. Changes in intense precipitation over the Central United States. J. Hydrometeorol. 13(1), 47-66.

Guo, X.S., Sinclair, T.R.,Ray, J.D., 1998. Effect of drought history on recovery of transpiration, photosynthesis, and leaf area development in maize. Soil Crop Sci. Soc. Fla. Proc. 57, 83-87.

Gutierrez-Lopez, J., Asbjomsen, H., Helmers, M.,Isenhart, T., 2014. Regulation of soil moisture dynamics in agricultural fields using strips of native prairie vegetation. Geoderma. 226, 238-249.

Hernandez-Santana, V. et al., 2013. Native prairie filter strips reduce runoff from hillslopes under annual row-crop systems in Iowa, USA. J. Hydrol. 477, 94-103.

Hura, T., Grzesiak, S., Hura, K., Grzesiak, M.,Rzepka, A., 2006. Differences in the physiological state between triticale and maize plants during drought stress and followed rehydration expressed by the leaf gas exchange and spectrofluorimetric methods. Acta Physiol. Plant. 28(5), 433-443.

Inamullah,Isoda, A., 2005. Adaptive responses of soybean and cotton to water stress - I. Transpiration changes in relation to stomatal area and stomatal conductance. Plant. Prod. Sci. 8(1), 16-26.

Jasechko, S. et al., 2013. Terrestrial water fluxes dominated by transpiration. Nature. 496(7445), 347-351.

Karl, T.R.,Knight, R.W., 1998. Secular trends of precipitation amount, frequency, and intensity in the United States. Bull. Am. Meterol. Soc. 79(2), 231-241.

Kim, J.,Verma, S.B., 1991. Modeling stomatal conductance in a temperate grassland ecosystem. Agric. For. Meteorol. 55(1-2), 149-166.

Le, P.V.V., Kumar, P.,Drewry, D.T., 2011. Implications for the hydrologic cycle under climate change due to the expansion of bioenergy crops in the Midwestern United States. Proc. Natl. Acad. Sci. U. S. A. 108(37), 15085-15090.

Liu, F.L., Jensen, C.R.,Andersen, M.N., 2003. Hydraulic and chemical signals in the control of leaf expansion and stomatal conductance in soybean exposed to drought stress. Funct. Plant Biol. 30(1), 65-73.

Lovisolo, C., Perrone, I., Hartung, W.,Schubert, A., 2008. An abscisic acid-related reduced transpiration promotes gradual embolism repair when grapevines are rehydrated after drought. New. Phytol. 180(3), 642-651.

Martin, C.E., Harris, F.S.,Norman, F.J., 1991. Ecophysiological response of C_3 forbs and C_4 grasses to drought and rain on a tallgrass prairie in Northeastern Kansas. Bot. Gazette. 152(3), 257-262.

Mishra, V., Cherkauer, K.A.,Shukla, S., 2010. Assessment of drought due to historic climate variability and projected future climate change in the Midwestern United States. J. Hydrometeorol. 11(1), 46-68.

Miyashita, K., Tanakamaru, S., Maitani, T.,Kimura, K., 2005. Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. Environ. Exp. Bot. 53(2), 205-214.

Nangia, V., Mulla, D.J.,Gowda, P.H., 2010. Precipitation changes impact stream discharge, nitrate-nitrogen load more than agricultural management changes. J. Environ. Qual. 39(6), 2063-2071.

Pirasteh-Anosheh, H., Emam, Y.,Pessarakli, M., 2013. Changes in endogenous hormonal status in corn (*Zea mays*) hybrids under drought stress. J. Plant Nutr. 36(11), 1695-1707.

Pryor, S.C., Howe, J.A.,Kunkel, K.E., 2009. How spatially coherent and statistically robust are temporal changes in extreme precipitation in the contiguous USA? Int. J. Climatol. 29(1), 31-45.

Radke, J.K.,Berry, E.C., 1993. Infiltration as a tool for detecting soil changes due to cropping, tillage and grazing livestock. American Journal of Alternative Agriculture. 8(4).

Randall, G.W.,Mulla, D.J., 2001. Nitrate nitrogen in surface waters as influenced by climatic conditions and agricultural practices. J. Environ. Qual. 30(2), 337-344.

Ray, J.D.,Sinclair, T.R., 1997. Stomatal closure of maize hybrids in response to drying soil. Crop Sci. 37(3), 803-807.

Ray, J.D.,Sinclair, T.R., 1998. The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. J. Exp. Bot. 49(325), 1381-1386.

Ripley, B., Frole, K.,Gilbert, M., 2010. Differences in drought sensitivities and photosynthetic limitations between co-occurring C_3 and C_4 (NADP-ME) Panicoid grasses. Ann. Bot. 105(3), 493-503.

Sauer, T.J., Singer, J.W., Prueger, J.H., DeSutter, T.M.,Hatfield, J.L., 2007. Radiation balance and evaporation partitioning in a narrow-row soybean canopy. Agric. For. Meteorol. 145(3-4), 206-214.

Schachtman, D.P.,Goodger, J.Q.D., 2008. Chemical root to shoot signaling under drought. Trends Plant Sci. 13(6), 281-287.

Schilling, K.E.,Jacobson, P., 2010. Groundwater conditions under a reconstructed prairie chronosequence. Agr. Ecosyst. Environ. 135(1-2), 81-89.

Schmidt, J.J., Blankenship, E.E.,Lindquist, J.L., 2011. Corn and velvetleaf (*Abutilon theophrasti*) transpiration in response to drying soil. Weed Sci. 59(1), 50-54.

Senock, R.S.,Ham, J.M., 1995. Measurements of water use by prairie grasses with heat balance sap flow gauges. J Range Manage. 48(2), 150-158.

Serraj, R., Allen, L.H.,Sinclair, T.R., 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. Global Change Biol. 5(3), 283-291.

Seversike, T.M., Sermons, S.M., Sinclair, T.R., Carter, T.E.,Rufty, T.W., 2014. Physiological properties of a drought-resistant wild soybean genotype: Transpiration control with soil drying and expression of root morphology. Plant Soil. 374(1-2), 359-370.

Steffens, K.J.,Franz, K.J., 2012. Late 20th-century trends in Iowa watersheds: an investigation of observed and modelled hydrologic storages and fluxes in heavily managed landscapes. Int. J. Climatol. 32(9), 1373-1391.

Swemmer, A.M., Knapp, A.K.,Smith, M.D., 2006. Growth responses of two dominant C_4 grass species to altered water availability. Int. J. Plant Sci. 167(5), 1001-1010.

Tardieu, F.,Davies, W.J., 1992. Stomatal response to abscisic acid is a function of current plant water status. Plant Physiol. 98(2), 540-545.

Todd, C.E.D., Harbor, J.M.,Tyner, B., 2006. Increasing magnitudes and frequencies of extreme precipitation events used for hydraulic analysis in the Midwest. J. Soil Water Conserv. 61(4), 179-185.

Tomer, M.D.,Schilling, K.E., 2009. A simple approach to distinguish land-use and climate-change effects on watershed hydrology. J. Hydrol. 376(1-2), 24-33.

Turner, C.L.,Knapp, A.K., 1996. Responses of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecology. 77(6), 1738-1749.

Turner, N.C., 1991. Measurement and influence of environmental and plant factors on stomatal conductance in the field. Agric. For. Meteorol. 54(2-4), 137-154.

Villarini, G., Smith, J.A.,Vecchi, G.A., 2013. Changing frequency of heavy rainfall over the Central United States. J. Clim. 26(1), 351-357.

Vitale, L. et al., 2009. Growth and gas exchange response to water shortage of a maize crop on different soil types. Acta Physiol. Plant. 31(2), 331-341.

Vitkauskaite, G.,Venskaityte, L., 2011. Differences between C_3 (*Hordeum vulgare* L.) and C_4 (*Panicum miliaceum* L.) plants with respect to their resistance to water deficit. Zemdirbyste-Agriculture. 98(4), 349-356.

Wang, C., Yang, A., Yin, H.,Zhang, J., 2008. Influence of water stress on endogenous hormone contents and cell damage of maize seedlings. J. Integr. Plant Biol. 50(4), 427-434.

Wang, L., Zhang, T.,Ding, S., 2006. Effect of drought and rewatering on photosynthetic physioecological characteristics of soybean. Acta Ecol. Sin. 26(7), 2073-2078.

Xu, Z., Zhou, G.,Shimizu, H., 2010. Plant responses to drought and rewatering. Plant Signaling Behav. 5(6), 649-54.

Zhou, X. et al., 2014. Nutrient removal by prairie filter strips in agricultural landscapes. J. Soil Water Conserv. 69(1), 54-64.

Table 1. Sowing date for each species in the study, days after sowing (das) when experiments were started, and average leaf area for the plants in all treatments at the end of each experiment.

Species	Sowing date	Beginning of experiments (das)			Average leaf area (cm^2)		
		Age 1	Age 2	Age 3	Age 1	Age 2	Age 3
G. max	May-07-13	49	63	74	2448.16	3007.74	2708.23
Z. mays	May-07-13	92			2897.35		
A. geradii	Jan-01-13	224	233	241	116.60	83.19	101.81
S. canadensis	Dec-15-12	257	262	268	775.93	657.47	645.65

Table 2. ANOVA results (Type III) for the effect of treatments and age on daily transpiration in plants of *G. max*, *Z. mays*, *A. gerarii* and *S. canadensis*. Bolded numbers and star show significant effects at $P < 0.05$.

Species	Effect	F value	*P*
G. max	Treatment	4.32	**0.019**
	Age	7.81	**0.001**
Z. mays	Treatment	2.97	0.084
A. gerardii	Treatment	6.59	**0.003**
	Age	15.96	**<0.001**
S. canadensis	Treatment	6.13	**0.005**
	Age	0.34	0.717

Figure 1. Schematic representation of vertical sectioning in a *G. max* plant. Leaves in the rectangle area were collected for predawn water potential measurements. Same approach was used in *Z. mays*, *A. gerardii* and *S. canadensis*.

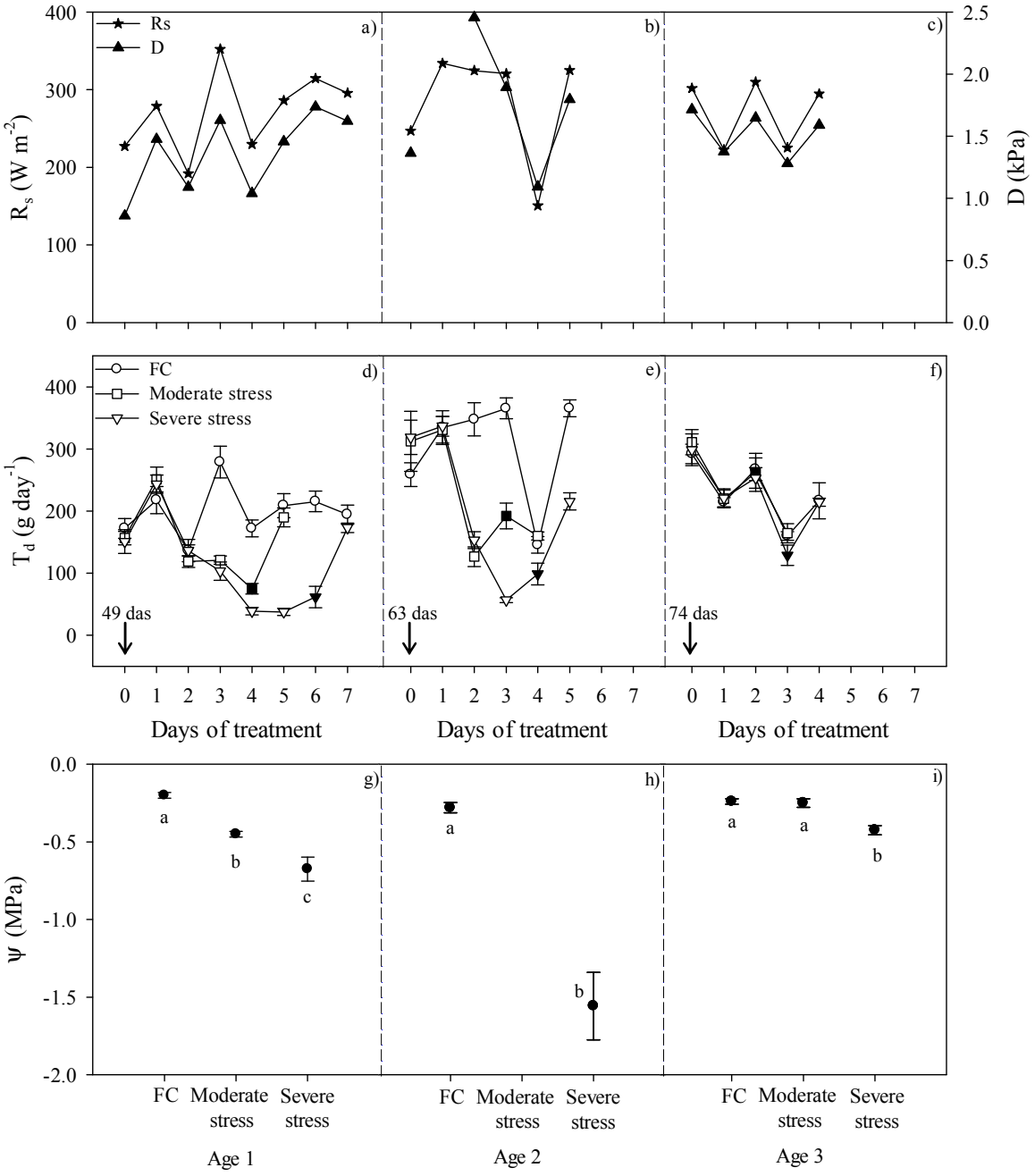


Figure 2. Daily average solar radiation (R_s) and vapor pressure deficit (D), daily transpiration (T_d), and plant water potential (Ψ) in age 1(a, d and g, respectively), age 2 (b, e, and h) and age 3 (c, f, and i) in the *G. max* experiment. Dates for each experiment are: June 25-July 2, July 9-14, and July 20-24, 2013. Filled symbols in d, e and f show days when plants were rewatered. Error bars represent SE of the mean. Letters in g, h and i indicate significant differences among means ($P < 0.05$).

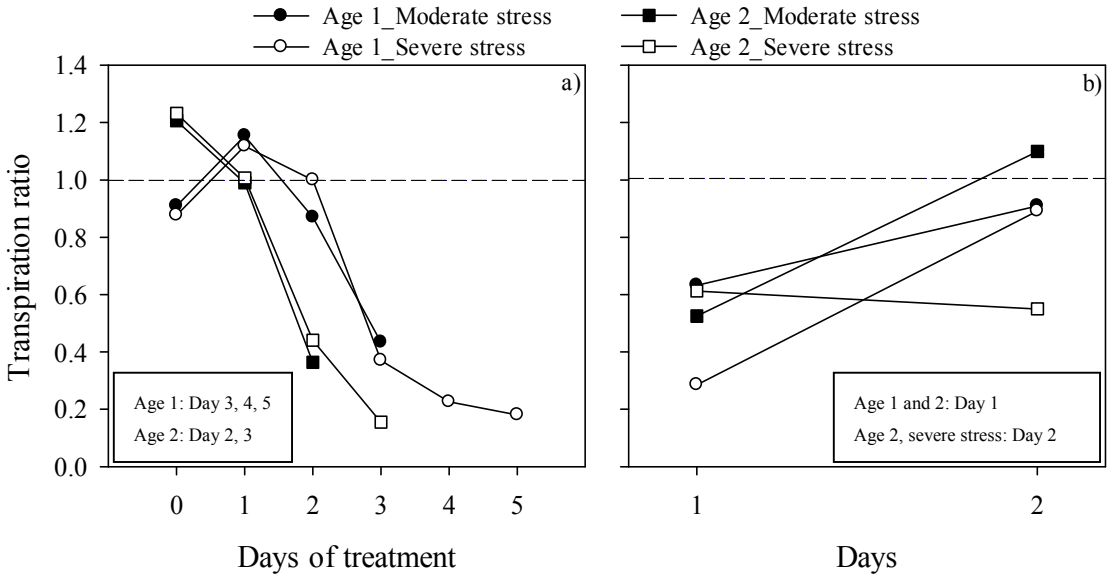


Figure 3. Daily transpiration ratio in *G. max* plants during the soil dry-down process (a) and response to rewatering (b) after moderate and severe water stress. Days when T_d in treated plants was significantly lower than in control plants ($P < 0.05$) are shown inside rectangles.

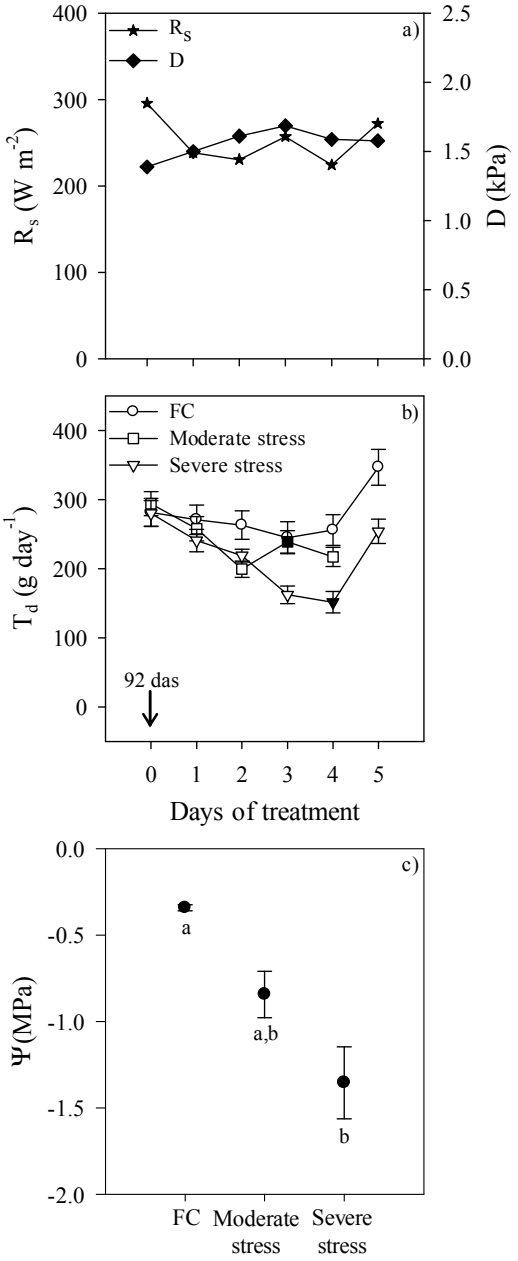


Figure 4. a) Daily average solar radiation (R_s) and vapor pressure deficit (D); b) daily transpiration (T_d); and c) plant water potential (Ψ) during August 7-12 in the *Z. mays* experiment. Filled symbols in b show days when plants were rewatered. Error bars represent SE of the mean. Letters in c indicate significant differences among means ($P < 0.05$).

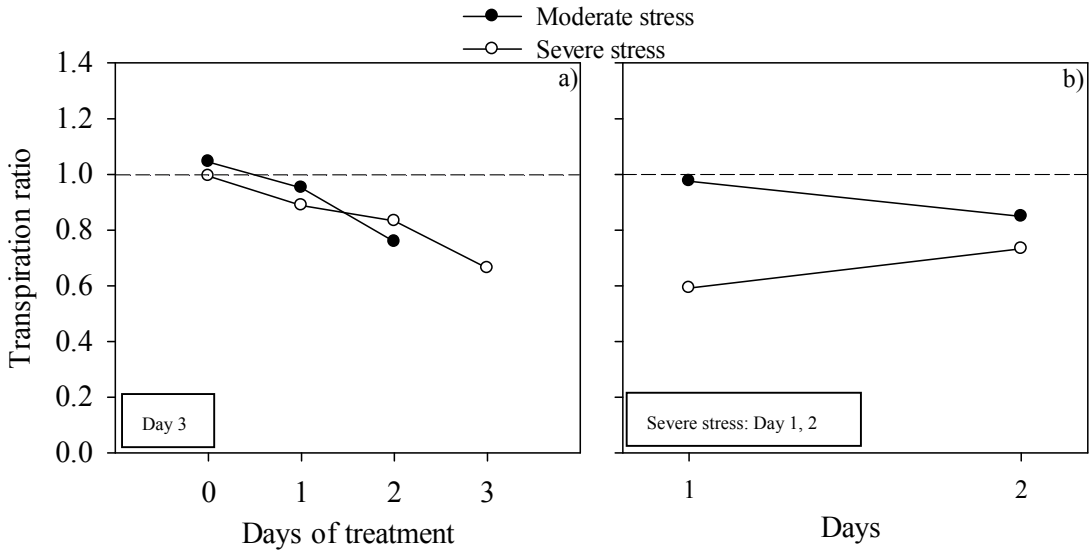


Figure 5. Daily transpiration ratio in *Z. mays* plants during the soil dry-down process (a) and response to rewatering (b) after moderate and severe water stress. Days when T_d in treated plants were significantly lower than in control plants ($P < 0.05$) are shown inside rectangles.

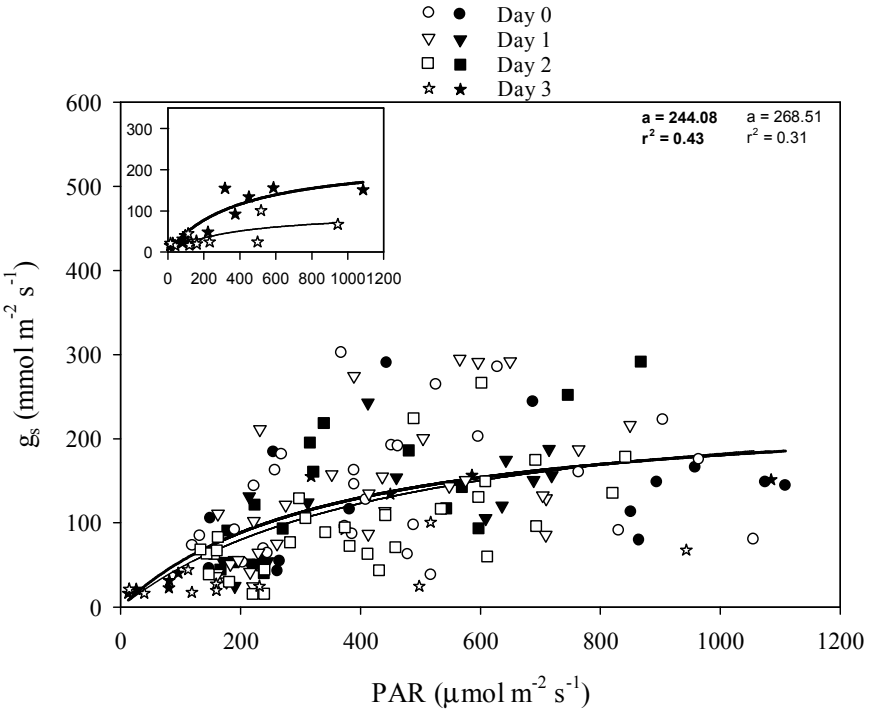


Figure 6. g_s/PAR curves for *Z. mays*. Each point represents an average of 3 measurements per plant collected from August 7-10. Plants belonging to moderate and severe water stress treatments where combined to obtain a single curve for the water stress effect. Bold letters, filled symbols and the thick line correspond to the control group. The opposite is for water-stressed plants.

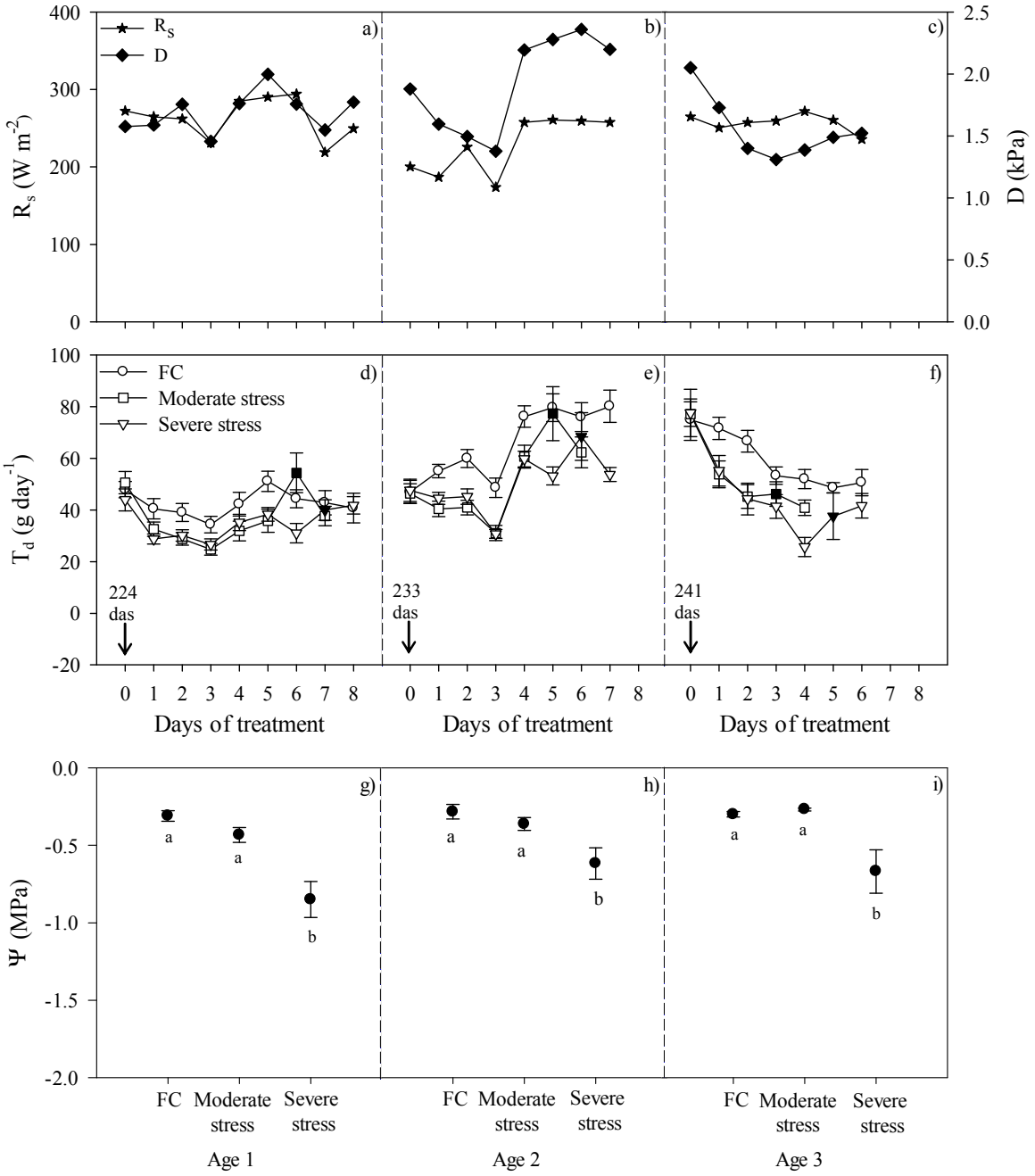


Figure 7. Daily average solar radiation (R_s) and vapor pressure deficit (D), daily transpiration (T_d), and plant water potential (Ψ) in age 1(a, d and g), age 2 (b, e, and h) and age 3 (c, f, and i) in the *A. gerardii* experiment. Dates for each experiment are: August 12-20, August 21-28, and August 29-September 4. Filled symbols in d, e and f show days when plants were rewatered. Error bars represent SE of the mean. Letters in g, h and i indicate significant differences among means ($P < 0.05$).

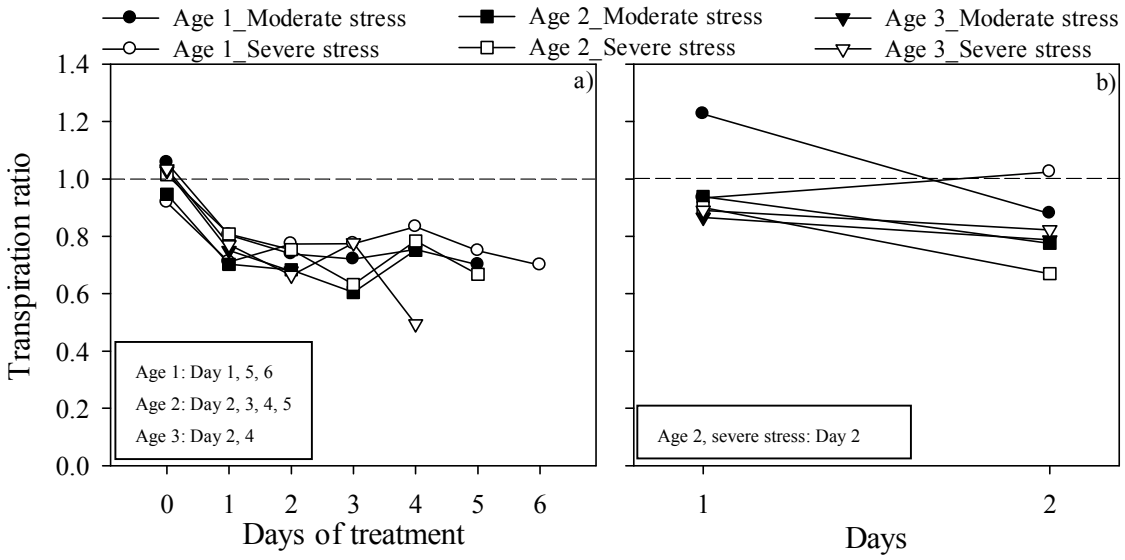


Figure 8. Daily transpiration ratio in *A. gerdardii* plants during soil dry-down process (a) and response to rewatering (b) after moderate and severe water tress. Days when T_d in treated plants was significantly lower than in control plants ($P < 0.05$) are shown inside rectangles.

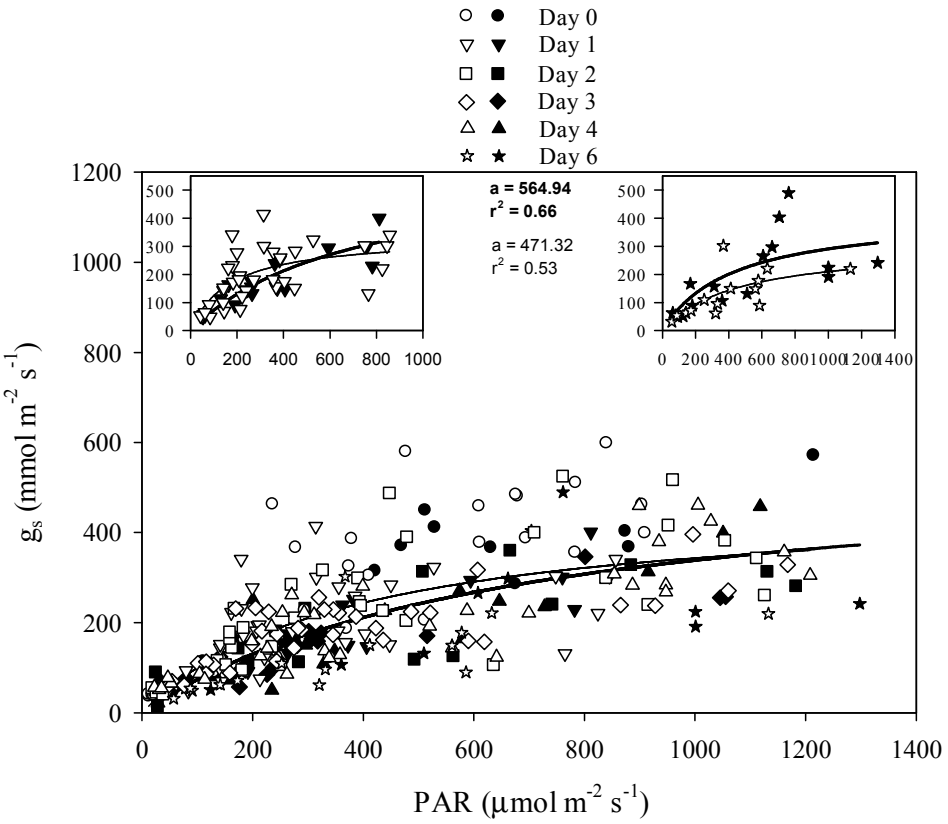


Figure 9. g_s/PAR curves for *A. gerardii*. Each point represents an average of 3 measurements per plant collected from August 12-18 (ge 1). Plants belonging to moderate and severe stress treatments where combined to obtain a single curve for the water stress effect. Bold letters, filled symbols and the thick line correspond to the control group. The opposite is for water-stressed plants.

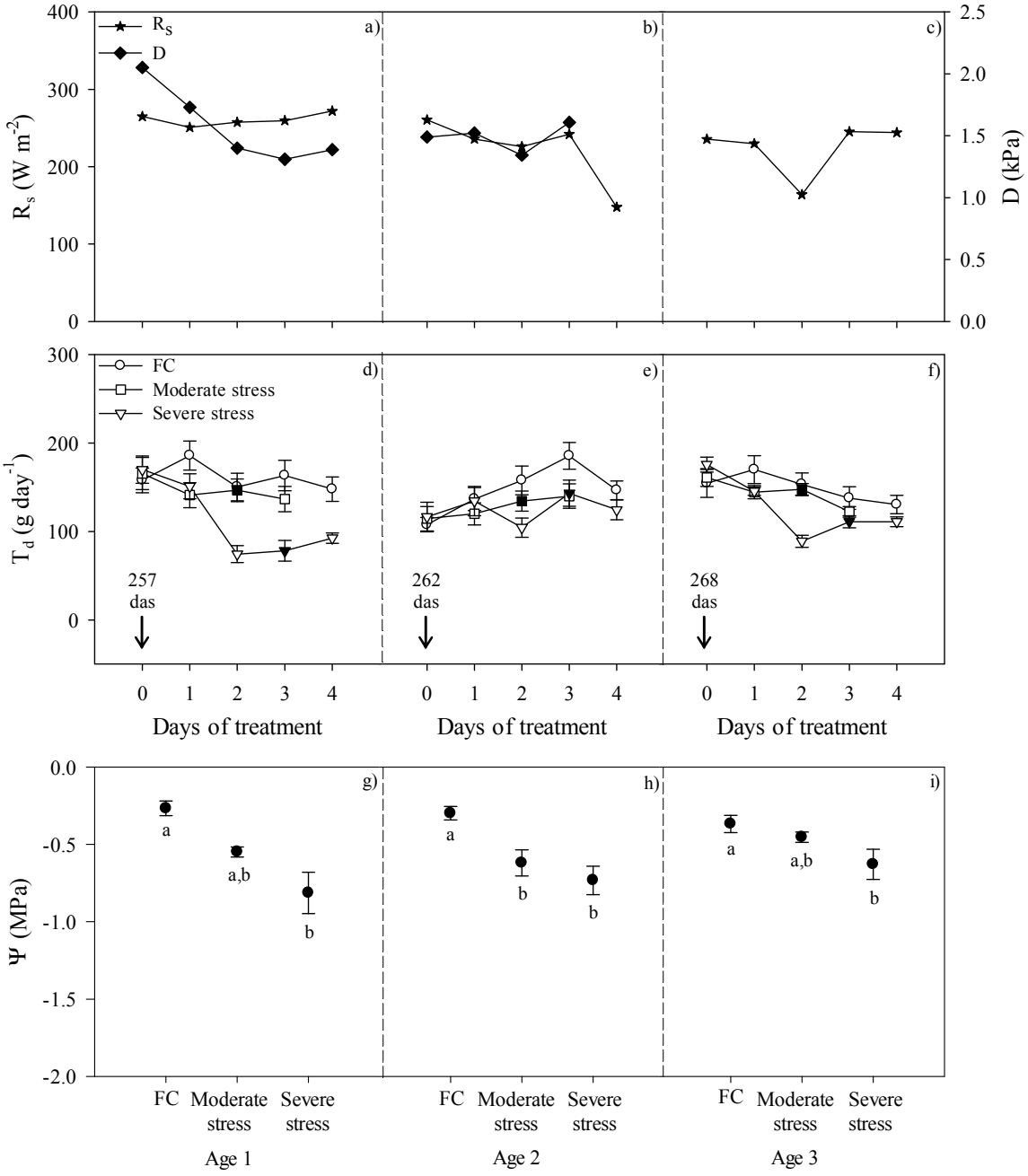


Figure 10. Daily average solar radiation (R_s) and vapor pressure deficit (D), daily transpiration (T_d), and plant water potential (Ψ) in age 1(a, d and g), age 2 (b, e, and h) and age 3 (c, f, and i) in the *S. canadensis* experiment. Dates for each experiment are: August 29-September 2, September 3-7, and September 9-13. Error bars represent SE of the mean. Filled symbols in d, e and f show days when plants were rewatered. Letters in g, h and i indicate significant differences among means ($P < 0.05$).

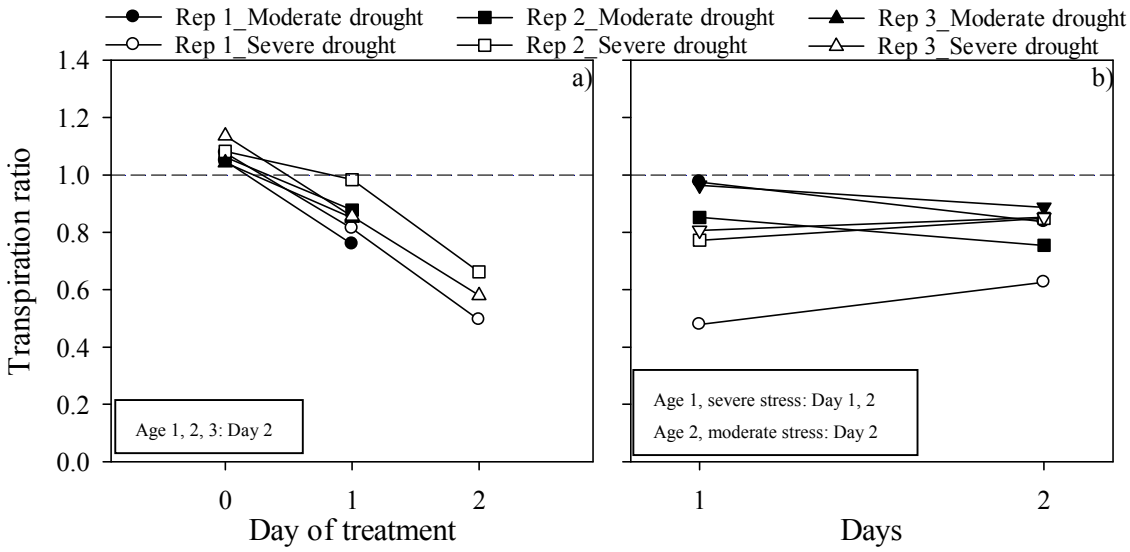


Figure 11. Daily transpiration ratio in *S. canadensis* plants during the soil dry-down process (a) and response to rewatering (b) after moderate and severe water stress. Days when T_d in treated plants was significantly lower than in control plants ($P < 0.05$) are shown inside rectangles.

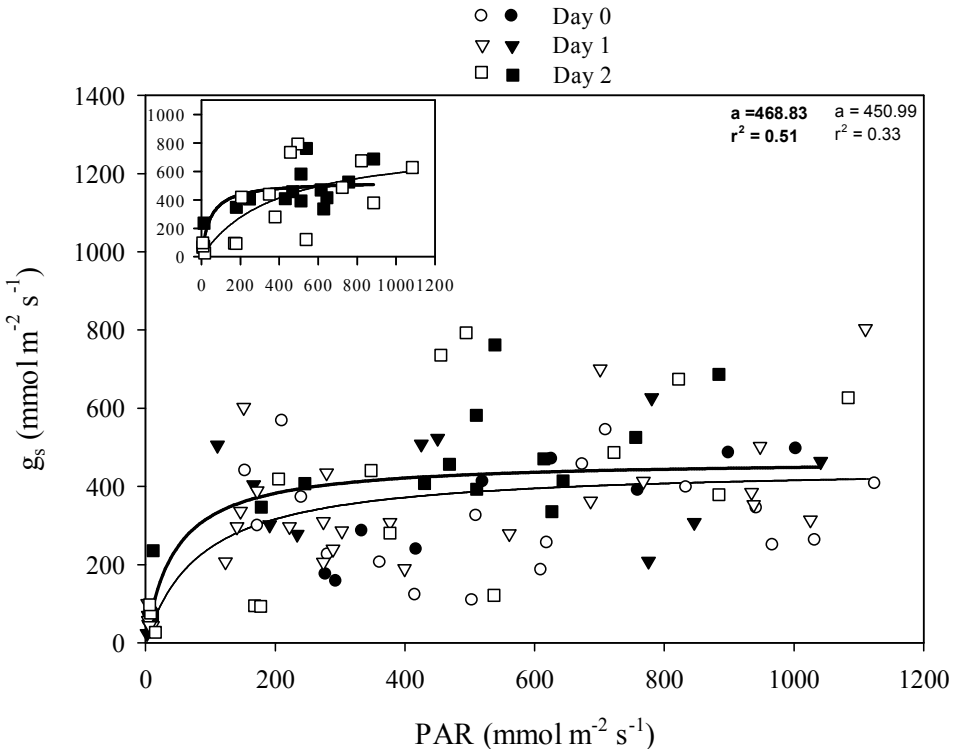


Figure 12. g_s/PAR curves for *S. canadensis*. Each point represents an average of 3 measurements per plant collected from September 3-5 (age 2). Plants belonging to moderate and severe water stress treatments where combined to obtain a single curve for the water stress effect. Bold letters, filled symbols and the thick line correspond to the control group. The opposite is for water-stressed plants.

CHAPTER 6: GENERAL CONCLUSIONS

The purpose of this research was to provide information that helps to understand how plant water use patterns in prairie vegetation at both the stand (evapotranspiration) and plant (transpiration) level may help to restore hydrologic regulation in intensive agriculture landscapes whose hydrologic processes, especially surface runoff, have been negatively impacted. The studies to accomplish our objectives were conducted under field and controlled conditions at the Neal Smith National Wildlife Refuge and in a greenhouse at Iowa State University, respectively.

In the first study field, evapotranspiration measurements were collected from a 5-year old restored prairie and an annual corn-soybean rotation crop field over two complete growing seasons (May 1- October 5 of 2007 and 2008). Higher evapotranspiration was found in the prairie compared to the crop fields both early and late in the growing season, suggesting that perennial vegetation can play an important role in increasing soil water storage capacity during typical wet springs. This study also showed that soil water content in the restored prairie remained lower than in the crop field. The transpiration rates of two dominant native prairie species (*Ratibida pinnata* and *Andropogon gerardii*) increased dramatically following a large precipitation event that occurred after two weeks of a relative absence of rain. These results support the contention that transpiration by native species may have a direct impact on mitigating runoff events.

In another field study, plant transpiration was measured at two topographic positions in a mixed annual-perennial watershed. Those data were used to identify which of four environmental variables, namely net radiation, vapor pressure deficit, soil water content, and

wind speed, are the main controllers of hourly transpiration in the most dominant prairie species (*Solidago canadensis*) growing in strips, and the adjacent crops *Glycine max* and *Zea mays*. In the two growing seasons of 2011 and 2012, which contrasted in precipitation conditions, net radiation was found to be the main driver of hourly transpiration as it explained 70-89% of transpiration variability in all the species. This outcome suggests that this one single variable could be used to predict transpiration during those days when data are missed due to equipment failures.

From the same study field, transpiration patterns and leaf area index in perennial strips located at two contrasting topographic positions were determined at different periods from July 8 to September 22 in 2011, and from June 7 to September 13 in 2012. This information was used to elucidate the potential impact of water use from *S. canadensis*, the most dominant prairie species, on the watershed hydrology. *Solidago canadensis* transpiration was higher in the strip located at the upslope position than at the footslope until August 7 and July 12 in 2011 and 2012, respectively. This finding is interesting as it advocates for a relevant role of the strip at the upland position to help increase soil water storage capacity in the first half of the growing season.

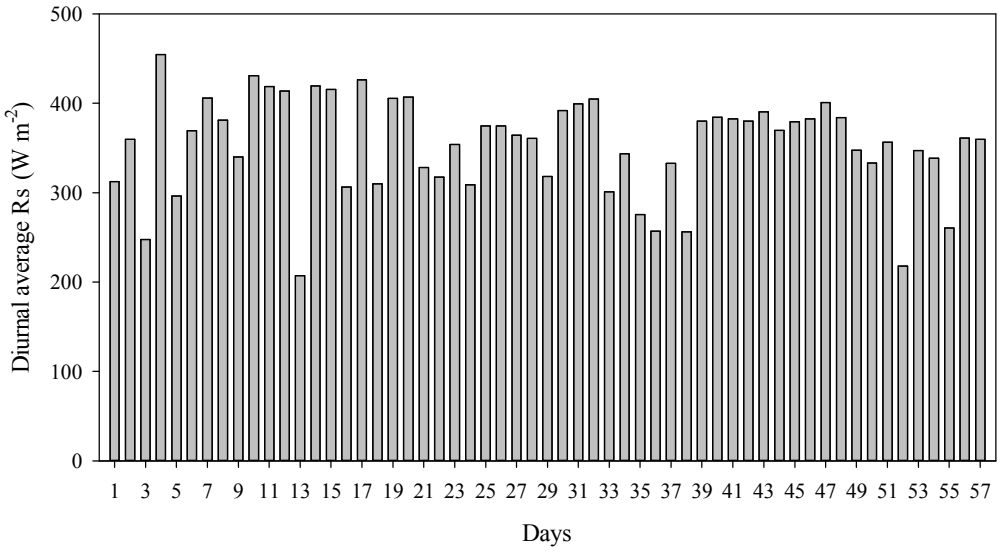
The greenhouse study assessed the responsiveness of two native prairie species (*S. canadensis* and *A. gerardii*) and two crops (*G. max* and *Z. mays*) to rewattering, after initiation of moderate and severe water stress levels. This study was conducted to reproduce the observations from the 2008 field study when it was found that two native prairie species increased their transpiration rate in response to a large precipitation event preceded by two dry weeks, but *Z. mays* did not. Results obtained in the greenhouse study were similar to that found in the field. The two native species showed a rapid recovery after the soil water

content returned to field capacity, regardless of the water stress intensity experienced. In contrast, the reaction in *Z. mays* was determined by the water stress level suffered by the plants, and *Glycine max* always showed a delayed response.

Overall, this research showed that incorporation of native prairie vegetation into agricultural dominated landscapes can help to restore hydrologic process not only by supporting higher soil infiltration rates, as it is frequently assumed, but also by extracting more water from the soil when it is most needed.

APPENDIX A: DIURNAL AVERAGE R_S

This graph shows the diurnal average of solar radiation (R_s) for all the days when daily transpiration (T_d) was measured, which totaled 57 days. First and last day were June 25 and September 13, respectively.



APPENDIX B: ROOTS

Photos A and B correspond to roots of *G. max* plants, photos C and D show roots of *S. canadensis* and *A. gerardii*, respectively.

A

B

C

D